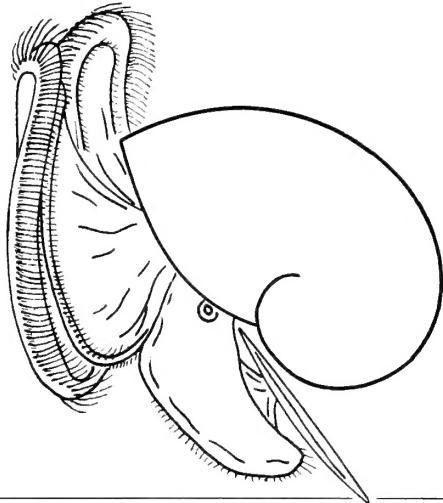






THE VELIGER

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Berkeley, California
R. Stohler (1901–2000), Founding Editor



Volume 44

January 2, 2001 to October 1, 2001

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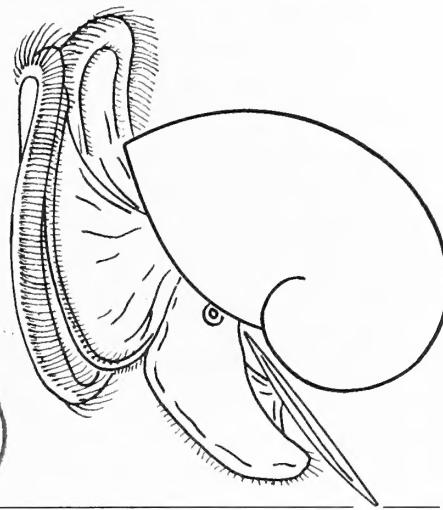
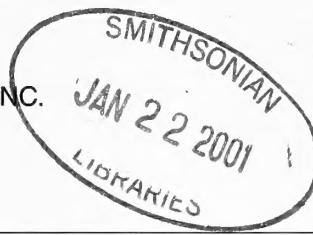
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THE VELIGER

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Very short papers, generally not over 750 words, will be published in a "Notes, Information & News" column; in this column will also appear notices of meetings and other items of interest to our members and subscribers.

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Shadow Responses and the Possible Role of Dermal Photoreceptors in the Hawaiian Black Snail, *Nerita picea* (Gastropoda: Neritidae)

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Abstract. The roles played by eyes, cephalic tentacles, and dermal receptors in the shadow responses of the Hawaiian black nerite gastropod, *Nerita picea*, were tested. Snails exhibited withdrawal responses when exposed to a passing shadow. Shadow responses involved a contraction of both cephalic tentacles and partial to full retreat of the snout or whole body into the shell. Removal of the cephalic tentacles or differentiated eyes did not impair the intensity of response to passing shadows. Withdrawal responses to passing shadows at very low light levels (1.1–320 lux) in blind and/or ablated snails demonstrated the maintenance of acute photoreceptivity. The observations presented here are consistent with the hypothesis that dermal photoreceptors are primarily responsible for the occurrence of shadow responses in *N. picea*.

INTRODUCTION

For the vast majority of animals, light is a distinctive stimulus that conveys, via sensory structures, useful information about the environment. In invertebrates, a wide range of specialized light receptors, which include compound eyes, ocelli, single-lens eyes, and simple eyes in the form of pigment cups and pinhole eyes, have evolved to facilitate light detection (Dusenberry, 1992). However, many marine invertebrates also show responses to light that are not mediated by any structurally known receptors. These responses are referred to as extraocular or dermal sensitivity to light. Dermal sensitivity to light has been observed in tubicolous polychaetes (Nicol, 1950), crustaceans (Larimer, 1966), echinoderms (Millot, 1954; Yoshida & Ohtsuki, 1966), and gastropods (Millot, 1968). Dermal photosensitivity in mollusks usually involves withdrawal responses that are mediated via sensitivity in the siphon, e.g., *Mya arenaria* (Light, 1930); the anterior edge of the mantle, e.g., *Helix* (Föh, 1932); or both the mantle edge and siphon, e.g., *Nassarius reticulatus* (Crisp, 1972). Many other gastropods also exhibit shadow responses that are mediated through dermal photoreceptors rather than differentiated eyes (Franz, 1921; Föh, 1932), leading Land (1984) to argue that defense responses of most mollusks to shadow stimuli are mediated through dermal photoreceptors.

Preliminary observations by one of us (LMG) suggested that the Hawaiian black nerite, *Nerita picea* (Récluz, 1841) (Gastropoda: Neritidae), a ubiquitous snail in the rocky intertidal of the Hawaiian Islands, responds to passing shadows by withdrawing into its shell. The pre-

sent study was designed to test the importance of dermal photoreceptors in the defense responses of *N. picea* to shadow stimuli. The possible role(s) played by eyes and/or cephalic tentacles in shadow responses was also assessed by using blinded snails and snails with ablated tentacles. Blinding and ablation experiments were felt necessary for a number of reasons: (1) A previous study (LMG, unpublished results) demonstrated that both negative phototaxis and vision are important in the accurate coastward orientation of *N. picea*, suggesting that negative photo-tactic responses, and consequently, shadow responses, might be visually mediated; (2) the eyes of most invertebrates possess pigment-bearing cells that are closely associated with photoreceptive cells (Goldsmith, 1972) and thus might be partially involved in shadow responses; (3) a common viewpoint has maintained that eyes might be the only photosensitive structures present in some snails; (4) it is known that the cephalic tentacles of other gastropods have a high degree of tactile sensitivity and may possess photosensitive abilities as well (Charles, 1966). The research we present here demonstrates that defense responses to shadow stimuli in *N. picea* are not mediated by either eyes or cephalic tentacles, but appear to be primarily controlled via dermal receptors that are associated with the pigmented surface areas of the snail's body.

MATERIALS AND METHODS

Experimental Animals

Nerita picea (Figure 1) has a globose shell with a low spire and an elliptical aperture. It has a broad snout with slightly thick lateral processes. Fully retractable cephalic tentacles are located on each side of the snout and the eye-stalks with apical eyes located on the outer side of

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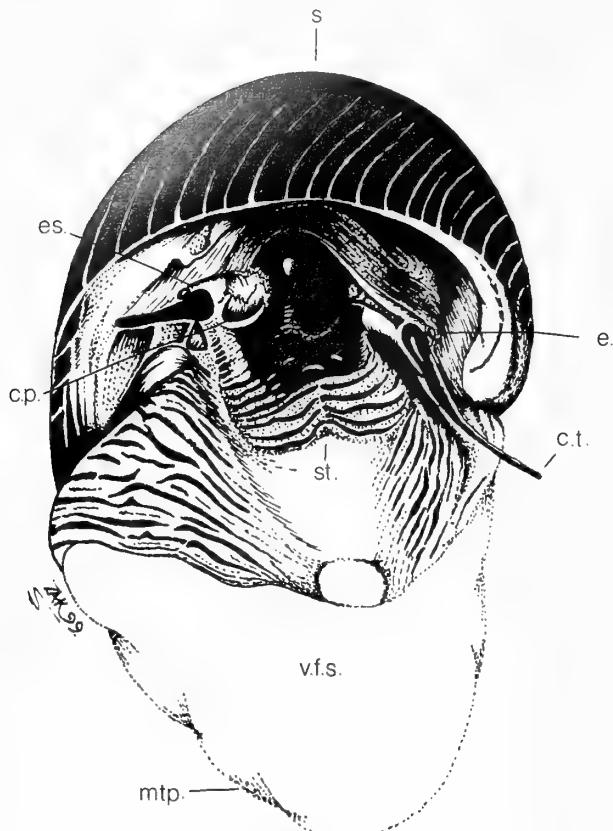


Figure 1

Ink illustration of *Nerita picea*. Key: c.p., cephalic penis; c.t., cephalic tentacle; e., eye; es., eye-stalk; mtp., metapodium; s., shell; st., snout; v.f.s., ventral foot sole. Drawing by C. Z. Womersley from a photograph by L. M. Gutiérrez.

these. The coloration of the animals is pale gray, with black pigmentation on the upper surface of the snout, the sides of the foot, the mantle edge, and in males, the cephalic penis. This pigmentation occurs in highly concentrated flecks that form horizontal black bands, or "tiger striping" (Figure 1). The cephalic tentacles carry long longitudinal black lines on the upper surface, but these fade toward the underside. The apical regions of the eye-stalk have a high concentration of pigmentation, which is not set in any distinct pattern. The sole of the foot is unpigmented. The snail carries the operculum on the posterior foot lobe (metapodium). When crawling, *N. picea* exposes part of its snout, both cephalic tentacles, and the eyes (not eye-stalks) at the edge of the shell.

Specimens of adult *N. picea* ($n = 4264$) were collected during morning low tides from two intertidal rocky shores, Sandy Beach and Pupukea, located on opposite sides on the island of O'ahu. The two sites were chosen to allow comparison of shadow responses by two different populations of snails from different substrates and ex-

posure. Sandy Beach is primarily composed of black volcanic boulders that are highly exposed to surf action. Conversely, Pupukea is mainly a limestone rocky shore with volcanic boulders dispersed throughout and is more sheltered from the effects of surf action due to the presence of a limestone bench offshore. The geomorphology of these two beaches has been discussed elsewhere (Wentworth, 1938, 1939). Snails were maintained in glass aquaria with running seawater and provided with a 12light:12dark cycle. Mean shell measurements for Sandy Beach and Pupukea snails were 12.11 mm (length), 9.7 mm (width), 6.57 mm (height); and 15.77 mm (length), 10.478 mm (width), and 7.457 mm (height), respectively. Individual sets of snails collected from both these sites were subjected to two series of experiments described below.

Shadow Response of Normal Snails

Three tests were devised to determine the shadow responses of various parts of the body: (1) "Crawling." In this position, snails exposed part of the snout, both cephalic tentacles, and the eyes at the edge of the shell, in addition to the anterior and lateral portions of the foot, i.e., maximal pigmentation exposure; (2) "Sole of Foot." Snails were turned upside down and allowed to emerge from the shell until the sole of the foot was maximally extended. In this position, the foot almost covered the entire shell, and no anterior, lateral, or posterior foot lobes were visible, i.e., minimal or no pigmentation exposure; (3) "Metapodium." Snails were turned upside down and allowed to retreat into their shells. Testing occurred when the snail emerged from the shell at a point when only the metapodium, to which the operculum is attached and carried, was visible, i.e., partial pigmentation exposure.

Representative individuals of both snail populations were placed in one of the above test positions and exposed to a shadow stimulus by passing a square black card (8 × 8 cm) through a light source, decreasing the illumination from an initial light level of 1.1–1400 to 0 lux. The stimulus period lasted approximately 1 second. A light source (100 watts) was located 0.75 m above the experimental animals inside a completely enclosed 2 × 1 × 1 m matte black box ensuring uniform illumination. Temperature effects of the light source on experimental subjects were nil. Light intensities, representing a gradation from full moon (1.1 lux) to dusk or dawn (1400 lux), were controlled via a previously calibrated dimmer and measured with a GE light meter (Model No. 27A). Shadow responses of individual snails were observed at six different light intensities (1.1, 110, 320, 540, 750, and 1400 lux). All experiments were conducted in a dark room at night to avoid interference from ambient light, and the observer wore black to negate reflection from clothing.

A snail's reaction to a passing shadow was scored as

either "response" or "no response." A simultaneous contraction of both tentacles and/or snails retreating into the shell constituted a positive response. All other behaviors were scored as "no response." Because of the rapid habituation of snails to sequentially repeated shadow stimuli (LMG, unpublished observations), individual snails were only tested once.

Shadow Response of Blinded and Ablated Snails

To discern whether the eyes or cephalic tentacles mediated shadow responses, snails of both populations were anesthetized for 15 min in 7.5% MgCl₂ and either (1) the cephalic tentacles or (2) the eyes and the eye-stalks removed with iridectomy dissecting micro-scissors. Surgically treated animals were allowed to recover for 24–48 hr before being exposed to shadow stimuli in one of the three test positions in an identical manner to that described for normal snails. Control experiments used snails previously anesthetized that had an incision in the basal area of the eye and tentacles.

Statistical Analysis

Chi-square tests were conducted to assess the significance of the difference in shadow responses by snails exposed to shadow stimuli in each of the three test positions. Shadow responses with probabilities less than 0.05 indicated that a response was dependent on the body area being tested.

RESULTS

Nerita picea displayed two common responses to passing shadows. First, when crawling, there was either (a) a simultaneous contraction of both cephalic tentacles, or (b) contraction of cephalic tentacles coupled with a partial to full retreat of the snout or whole body into the shell. Second, when turned upside down, snails only exhibited a partial or full retreat into the shell; cephalic tentacles were retracted in the shell in blind and normal snails. Interestingly, as snails turned over and made contact with the substratum, shadow stimulation did not arouse a withdrawal response, and turning continued until the snail was in the upright position. Type of habitat, volcanic versus limestone, did not affect the shadow responses of snails (Table 1), as shadow responses did not vary between snail populations from Pupukea or Sandy Beach. Thus, the data presented represents a pooling of both populations.

Shadow Response of Normal Snails

Nerita picea demonstrated withdrawal responses to a passing shadow, and both body position and light intensity affected the intensity of response (Figure 2a, Table 2). "Crawling" and "metapodium" snails exhibited a positive dependence on light intensity with respect to the number of shadow responses (Crawling, χ^2 : 64.75, n =

Table 1

Chi-Square test results assessing whether degree of responses to shadow stimuli by *N. picea* is independent of beach of origin. Snails were collected from Sandy Beach and Pupukea.

Test position	χ^2 ^a response	χ^2 ^a no response	No. of trials	P ^b
Crawling	0.566	4.812	198	NS ^b
Sole of Foot	10.857	3.325	198	NS ^b
Metapodium	1.823	0.184	198	NS ^b

^a χ^2 (0.05, 10) = 11.07.

^b NS = non significant differences, $P > 0.05$.

396, $P < 0.001$; Metapodium, χ^2 : 72.467, n = 396, $P < 0.001$) (Figure 2a). At low light intensities (1.1–540 lux), "metapodium" snails showed reduced responses compared to "crawling" snails, but at higher light levels (750 and 1400 lux), showed a similar number of responses (Figure 2a, Table 2). Conversely, the responses of "sole of foot" snails were highly reduced at all light intensities and therefore not dependent on light intensity (χ^2 : 10.923, n = 396, $P > 0.05$) (Figure 2a).

Shadow Responses of Blind and Ablated Snails

Both blind and ablated snails exhibited positive shadow responses that were dependent on light intensity in all three test positions (Figures 2b, c, Table 3).

Blinded Snails. Blind "crawling" snails exhibited more positive responses than blind "sole of foot" snails at all light intensities (Figure 2b). "Crawling" and "metapodium" snails showed similar responses at most light intensities, but at 110 and 540 lux, more "metapodium" snails failed to respond to a passing shadow. There was no significant difference ($P > 0.05$) between the negative shadow response of "sole of foot" and "metapodium" snails.

Ablated Tentacle Snails. Ablated "crawling" snails behaved similarly to "metapodium" snails at most light intensities (Figure 2c). More "sole of foot" snails failed to respond to a shadow than "crawling" or "metapodium" snails at most light intensities (320–1400 lux). At 110 lux, "metapodium" and "sole of foot" snails behaved similarly, showing more negative responses to shadow stimuli. Irrespective of test position, the majority of ablated tentacle snails failed to respond at low light levels (1.1 lux).

Comparison of responses between ablated/blind, normal/blind, and normal/ablated snails is presented in Table 4. With the exception of lower light intensities (1.1 and 320 lux) where more "crawling" blind snails showed positive responses to shadow (Table 4a), no differences were observed in the shadow responses of blind and ablated snails in the three test positions. Both normal and

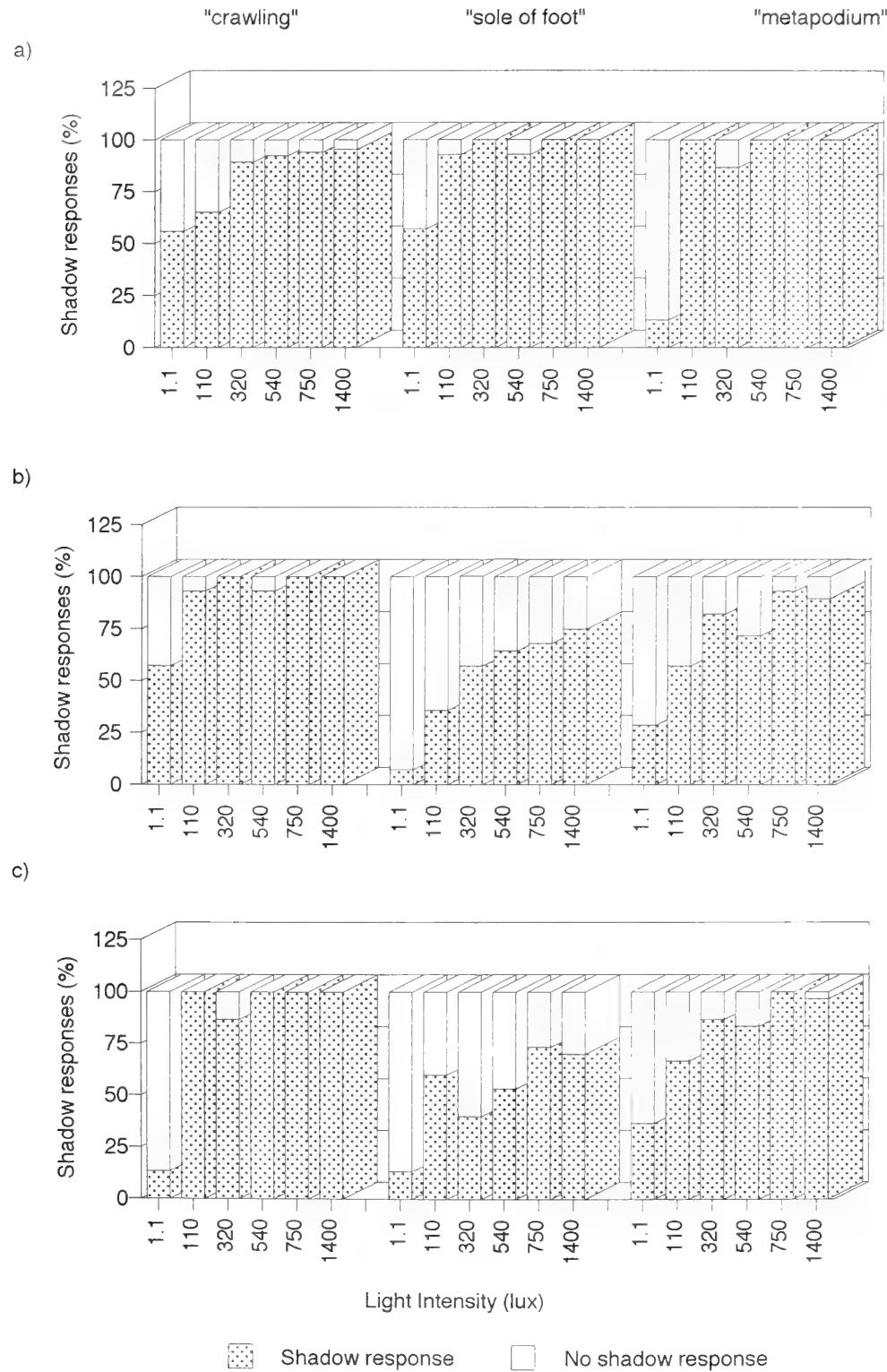


Figure 2

Shadow responses of adult *Nerita picea*. a) normal snails, b) blind snails, and c) snails with ablated tentacles.

Table 2

Chi-Square test results for shadow responses of normal snails (pooled data) in "crawling," "sole of foot," and "metapodium" positions tested.

Light intensity (lux)	Crawling ^a vs. sole of foot		Crawling vs. metapodium ^a		Sole of foot ^a vs. metapodium	
	χ^2 ^c	P	χ^2 ^c	P	χ^2 ^c	P
1.1	26.16	< 0.001	6.896	< 0.05	7.1249	< 0.05
110	19.049	< 0.001	9.827	< 0.01	1.6901	NS ^b
320	45.819	< 0.001	21.286	< 0.001	6.0789	< 0.05
540	37.562	< 0.001	14.687	< 0.001	6.8575	< 0.05
750	54.559	< 0.001	4.552	NS ^b	33.625	< 0.001
1400	53.387	< 0.001	0.151	NS ^b	50.256	< 0.001

^a N = 66 per light intensity.

^b NS = non significant differences, P > 0.05.

^c χ^2 (0.05, 2) = 5.991.

blind snails in either the "crawling" or "metapodium" position responded similarly to shadow at higher light intensities (Figures 2a, b, Table 4). At lower light intensities (110 lux), more "crawling" blind snails and less "metapodium" blind snails responded positively when compared to normal snails. In comparison to normal "sole of foot" snails, blind "sole of foot" snails showed more negative responses at most light intensities (320, 750, and 1400 lux). Shadow responses of blind "sole of foot" snails increased with increasing light intensity (Figure 2b). With the exception of low light levels (1.1 and 110 lux), shadow responses of normal and ablated snails in the "crawling" position were not significantly different (Table 4c). Unlike normal snails, more "metapodium" ablated snails failed to respond to a passing shadow at 110, 320, and 540 lux. The shadow responses of "metapodium" ablated snails increased with increasing light intensity (Figure 2c).

DISCUSSION

In the present study, *N. picea* from two different habitats (Sandy Beach and Pupukea) exhibited similar withdrawal responses to passing shadows. Shadow responses showed little impairment when differentiated eyes and eye-stalks

or cephalic tentacles were removed, indicating that shadow responses in *N. picea* are mediated, in large part, by receptors other than the eyes. These results are entirely consistent with the observation that many molluscan responses to light are based on dermal receptors (Land, 1968). For example, the reactions of *N. reticulatus* to shadow were not affected by eye removal (Crisp, 1972), and shadow crossing the cephalic tentacles of *Helix* elicited no response, but the animal fully withdrew when shadow crossed the mantle near the base of the shell (Föh, 1932).

Snail posture studies (Figure 2) suggest that the dermal receptors involved are closely associated with the dark pigmentation, "tiger striping," of the foot (Figure 1). Consequently, snails in the "crawling" position which had more pigmented body areas exposed, i.e., snout, anterior, posterior, and lateral foot lobes, eyes and/or tentacles, if present, were generally more responsive to light irrespective of experimental treatment (Table 2). Conversely, the "metapodium" position, which only allowed snails to expose the highly pigmented posterior part of the metapodium, and "sole of foot" snails, which exposed only the unpigmented ventral foot surface, were less responsive to shadows. Thus, like the black garden slug *Arion ater*, in which the amount of porphyrin present (known to cause photosensitivity) is directly proportional to the amount of dark pigment in the integument (Kennedy, 1959), the amount of dermal pigmentation in *N. picea* would appear to be directly proportional to dermal photosensitivity. The importance of the dermal photosensory system of *N. picea* is emphasized by the fact that it allowed blind and ablated snails to keenly respond to shadow stimuli at very low light levels (1.1 lux), allowing them to conduct a correct defense response even in a dimly lit environment.

In conjunction with both ocular and dermal receptors, our results also suggest that the darkly pigmented cephalic tentacles may have a photosensory role in addition

Table 3

Chi-Square test results assessing independence of shadow responses to light intensity of blind and ablated snails.

Test position	Blind snails ^a		Ablated snails ^a	
	χ^2 ^b	P	χ^2 ^b	P
Crawling	45.7233	< 0.001	130.08	< 0.001
Sole of foot	36.211	< 0.001	29.8331	< 0.001
Metapodium	41.6327	< 0.001	60.2459	< 0.001

^a N = 198 per test position per experimental treatment.

^b χ^2 (0.05, 5) = 11.070.

Table 4

Chi-Square test results for shadow responses of snails in experimental treatments and positions.

Light intensity (lux)	Crawling		Sole of foot		Metapodium	
	χ^2 ^c	P	χ^2 ^c	P	χ^2 ^c	P
a) Ablated vs. Blind Snails^a						
1.1	12.304	< 0.001	0.598	NS ^b	0.431	NS ^b
110	2.219	NS ^b	3.421	NS ^b	0.558	NS ^b
320	4.010	< 0.05	1.705	NS ^b	0.226	NS ^b
540	0.130	NS ^b	0.541	NS ^b	1.180	NS ^b
750	0.093	NS ^b	0.210	NS ^b	2.219	NS ^b
1400	1.408	NS ^b	0.181	NS ^b	0.429	NS ^b
b) Normal vs. Blind Snails^a						
1.1	0.009	NS ^b	0.802	NS ^b	0.205	NS ^b
110	7.730	< 0.01	0.342	NS ^b	7.051	< 0.01
320	3.209	NS ^b	5.283	< 0.025	2.967	NS ^b
540	1.846	NS ^b	3.760	NS ^b	0.351	NS ^b
750	1.772	NS ^b	10.445	< 0.005	1.890	NS ^b
1400	1.315	NS ^b	12.729	< 0.001	0.039	NS ^b
c) Normal vs. Ablated Snails^a						
1.1	15.389	< 0.001	0.002	NS ^b	0.102	NS ^b
110	13.748	< 0.001	0.943	< 0.005	6.864	< 0.01
320	0.151	NS ^b	0.612	NS ^b	10.073	< 0.005
540	2.398	NS ^b	0.989	NS ^b	6.234	< 0.025
750	1.897	NS ^b	14.375	< 0.001	3.300	NS ^b
1400	1.408	NS ^b	10.265	< 0.005	0.311	NS ^b

^a N = 66 (normal snails) and N = 33 (blind or ablated snails) per light intensity.^b NS = non significant differences, P > 0.05.^c χ^2 (0.05, 1) = 3.84.

to their accepted chemo- and mechano-sensory functions (Charles, 1966). Thus, blind snails (with tentacles) demonstrated more shadow responses at low light levels than did ablated snails (with eyes). However, the photosensory role of the cephalic tentacles appears to be extremely specific, enhancing the snail's dermal photosensitivity only at low light levels (1.1 lux).

Although the sole of the foot in *N. picea* is devoid of dark pigmentation, snails in the "sole of foot" position did show some responsiveness to shadow, suggesting the presence of photoreceptors not associated with pigment granules. Similar structures, called "phaosomes" (Haszprunar, 1996), are well known in annelids (Rhodes, 1991; Jamieson, 1992; Verger-Bocquet, 1992), bivalves (Salvini-Plawen & Mayr, 1977), and gastropods (Crisp, 1971; Kunz & Haszprunar, 1992). It is also possible, that photoreception in *N. picea* is not totally confined to specialized photosensitive structures or receptors. For example, some cnidarians which lack specialized photoreceptors are photosensitive (Passano & McCullough, 1962; Mackie & Boag, 1963; Mackie, 1975), and brain neurons can act as photoreceptors and may even possibly control the diurnal rhythm of locomotion in *Aplysia* (Land, 1984).

The results presented suggest two important functions that dermal photosensitivity fulfills. First, in conjunction

with the skoto-tactic responses, snails exhibit (LMG, unpublished observations), dermal photosensitivity which would appear to allow *N. picea* to mediate all phototactic responses and ensure that the snails optimize their location in their preferred habitat. Second, because *N. picea* lives in habitats that vary little in temperature, but can be cloudy for extended periods, it is evolutionarily advantageous for the species to possess an acute photosensitive mechanism that immediately alarms them of any changes in illumination caused by potential moving predators even at low light intensities. Present research is directed toward determining the relative importance of each component of the integrated photosensitive system that *N. picea* appears to use.

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Influence of Vegetation Type on the Constitution of Terrestrial Gastropod Communities in Northwest Spain

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Abstract. We investigated the influence of three different vegetation types on the establishment of terrestrial gastropod communities in the northwest Iberian Peninsula, using both an ordination technique (Detrended Correspondence Analysis) and a classification technique (Two-Way Indicator Species Analysis) applied to a 498×47 site-by-species abundance matrix (total number of individuals 17,902). The results of these analyses indicate that meadow sites are characterized by a group of species comprising *Cionella lubrica* (Müller, 1774), *Nesovitrea hammonis* (Ström, 1765), and *Zonitoides excavatus* (Alder, 1830). Woodland sites are characterized by a group comprising *Columella aspera* Waldén, 1966, *Oxychilus alliarius* (Miller, 1822), *Acanthinula aculeata* (Müller, 1774), and *Punctum pygmaeum* (Draparnaud, 1801). *Vitrella contracta* (Westerlund, 1871), *Discus rotundatus*, and *Aegopinella nitidula* (Draparnaud, 1805) form a group of companion species to this latter community.

INTRODUCTION

The view that vegetation type affects the distribution of terrestrial gastropods has been advanced from various angles and conclusions by authors including Bába, 1974; Beyer & Saari, 1977; André, 1982; Štamol, 1991, 1993; Cowie et al., 1995, and Hermida et al., 1995. Some authors have suggested that distribution is not primarily related to vegetation but rather to litter characteristics (Bishop, 1977; Locasciulli & Boag, 1987). By contrast, other authors have gone so far as to define gastropod communities corresponding to specified phytosociological communities (Frank, 1981; Kornig, 1989; Štamol, 1992; Bába & Bagi, 1997). It has also been suggested that microhabitat characteristics are the most important determinants of gastropod distribution (Drozdowski, 1968; Boag & Wishart, 1982; Young & Evans, 1991).

Most studies in this field are based on simple descriptions of the habitats in which different gastropod species are found, and relatively few studies have applied quantitative methods. In the present study, with the aim of furthering understanding of the influence of vegetation type on the distribution of terrestrial gastropods, we collected 498 samples from three biotopes (woodland, meadow, riverbank) in the northwest Iberian Peninsula (Figure 1). These three biotopes have distinct characteristics, and could be expected to have distinct malacofaunas. The data were analyzed with the aid of an ordination technique

(Detrended Correspondence Analysis) and a hierarchical classification technique (TWINSPAN).

DESCRIPTION OF THE STUDY AREA

The study area ($12,400 \text{ km}^2$) comprises the Provinces of A Coruña and Pontevedra in western Galicia (northwest Spain) (Figure 1). This area is bounded to the east by a mountain system running north-south and reaching elevations of up to 1100 m. Soils are generally poor, in view of the predominance of granites and schists, together with the high rainfall and hilly topography: cambisols, leptosols, and regosols are the most frequent. Climate is oceanic, characterized by high rainfall and mild temperatures. The potential vegetation over most of the study area (which falls within the Eurosiberian Region) is *Quercus robur* L. woodland. Depending on series, the codominant tree species may be *Betula pubescens* Ehrn. or *Castanea sativa* Miller, with *Laurus nobilis* L., *Ilex aquifolium* L., *Crataegus monogyna* Jacq., or *Frangus alnus* Miller in the shrub layer. However, much of the study region is currently occupied by the introduced species *Pinus pinaster* Aiton, *P. radiata* D., and *Eucalyptus globulus* Labill.

Riverbank vegetation is strongly influenced by groundwater level, with two different associations being recognized, both dominated by *Alnus glutinosa* (L.), namely *Valeriano pyrenaicae-Alnetum glutinosae*, richer in ferns

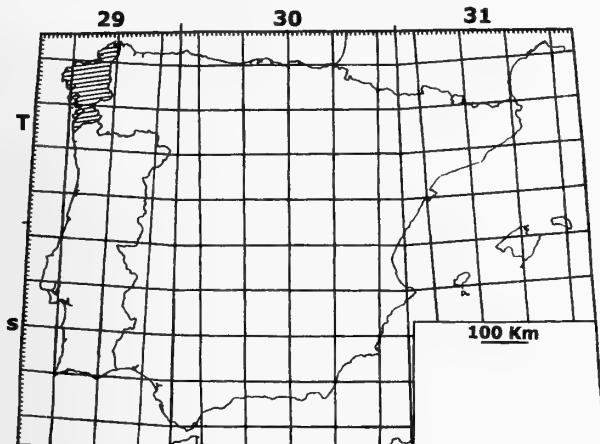


Figure 1

Location of the study area showing the 100 km squares of the UTM (Universal Transversal Mercator) Grid.

and nemoral herbs, and the more disturbed *Senecio bayonensis-Alnetum glutinosae*.

Meadow vegetation in the study area falls into the phytosociological class *Molinio-Arrhenatheretea elatioris*. The most frequent species within this association include *Agrostis capillaris* L., *Linum bienne* Miller, *Lolium perenne* L., *Trifolium dubium* Sibth., *Bellis perennis* L., *Plantago lanceolata* L., and *Holcus lanatus* L.

MATERIALS AND METHODS

Samples were collected, by stratified random sampling, from a total of 498 woodland, riverbank, and meadow sites (166 sites in each biotope). At each site we obtained a soil and litter sample of $100 \times 50 \times 5$ cm (length \times width \times depth). In the laboratory, the samples were wet-sieved through a 7 mm mesh over a 0.5 mm mesh. Material retained by the second sieve was carefully examined under a magnifying glass, with the aim of finding all gastropods. Gastropods found were immersed in water, then fixed in 70° alcohol. Only live specimens were included, since otherwise the abundance of testaceous species is likely to be overestimated (André, 1981; Phillipson & Abel, 1983). The 47 species found, together with the species codes used in the tables and figures, are listed in Appendix I.

The resulting 498×47 site-by-species abundance matrix was analyzed by Detrended Correspondence Analysis. DCA is a modification of Correspondence Analysis (CA) developed to overcome some conspicuous faults. The main modification, from which the technique obtains its name, is detrending, which attempts to remove the "arch effect" in which the second and subsequent axes appear as polynomial functions of the first axis and thus obscure the underlying gradient structure (Ter Braak, 1986, 1988).

The analysis was performed with CANOCO 3.1 (Ter Braak, 1990) using the rare-species downweighting option, by which all species with frequency below 20% of the maximum frequency of any species are downweighted in proportion to their frequency (Hill, 1979). For this analysis, the data matrix was first log-transformed ($\log[n + 1]$, where n is number of individuals).

CANOCO can supply centroids (weighted averages) of environmental variables in the ordination diagram. To find out the centroids, a matrix was built in which the variable biotope was converted into a nominal variable, so that it was possible to represent it by points in the ordination diagram (Ter Braak, 1988).

To verify the results obtained by ordination, we used a divisive hierarchical classification technique (Two-Way Indicator Species Analysis, TWINSPAN; Hill, 1979).

One of the basic ideas in TWINSPAN stems is that each group of sites can be characterized by a group of differential species, species that appear to prevail in one side of a dichotomy. The idea of a differential species is essentially qualitative, and to be effective with quantitative data must be replaced by a quantitative equivalent. This equivalent is the "pseudospecies." Each species abundance is replaced by the presence of one or more pseudospecies. The more abundant a species is, the more pseudospecies are defined. The levels of abundance that are used in TWINSPAN to define the crude scale are here termed "pseudospecies cut levels."

RESULTS

Ordination

The results of correspondence analysis of the log-transformed 498×47 site-by-species matrix are summarized in Figure 2 and Tables 1 and 2. The first four axes explained the majority of total variance. Significance was calculated using a χ^2 procedure.

Absolute contribution values for each species were calculated according to Judez (1989). Assuming that the 47 taxa have the same absolute contribution (defined as uniform absolute contribution), every species would contribute with 2.12% to the total variance of a single axis (100/47). Species with absolute contribution value higher than 2.12% would be the ones which better explain the axes (Judez, 1989). Such species are listed for axes I and II in Table 3.

The interpretation of the results of this analysis in terms of potential cause-effect hypotheses is made difficult by the large number of samples and species, and by the low inertias of the first three axes (despite their statistical significance). With the aim of reducing data noise and better revealing the data structure, we thus performed a second analysis (Figure 3) using those species that were not downweighted, i.e., species that had been assigned a downweighting factor of 1, namely, *Acanthinula aculeata*, *Arion intermedius*, *Aegopinella nitidula*, *Coumella as-*

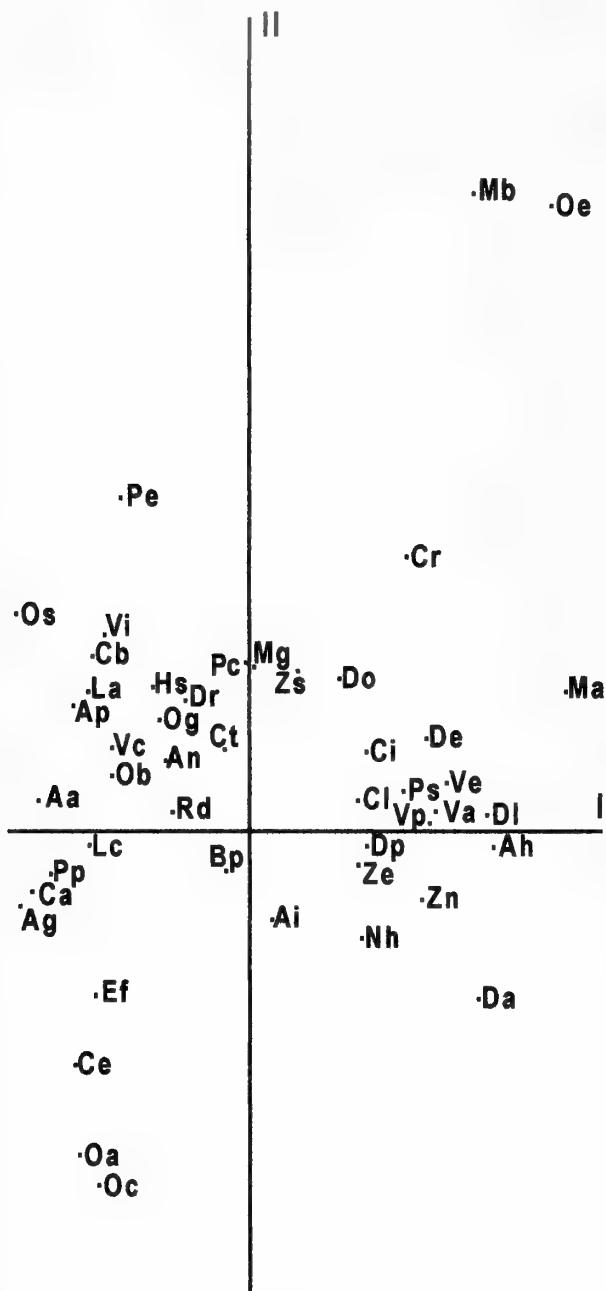


Figure 2

Ordination of the 47 species on the first two axes extracted by Detrended Correspondence Analysis.

pera, *Cionella lubrica*, *Carychium tridentatum*, *Discus rotundatus*, *Nesovitrean hammonis*, *Oxychilus alliarjus*, *Punctum pygmaeum*, *Vitrean contracta* and *Zonitoides excavatus* (Table 1). Eigenvalues (measure of separation of the species distributions along the ordination axis), percentage inertias, χ^2 values, and degrees of freedom are listed in Table 4.

Table 1

Downweighting values for each of the 47 species, as calculated by CANOCO.

Aa	1.00	De	0.966	Os	0.355	Ma	0.095
Ai	1.00	Do	0.836	Pu	0.281	Eb	0.059
An	1.00	Ef	0.787	Zs	0.268	Ap	0.053
Ca	1.00	Ob	0.775	Ci	0.265	Ag	0.029
Cl	1.00	Ps	0.751	Oc	0.237	Ce	0.029
Ct	1.00	Dl	0.659	Ve	0.234	Da	0.029
Dr	1.00	Cb	0.656	Mg	0.203	Dp	0.029
Nh	1.00	Lc	0.650	Og	0.174	Pe	0.029
Oa	1.00	Hs	0.459	Vi	0.161	Rd	0.029
Pp	1.00	Vp	0.477	Ah	0.128	Va	0.029
Vc	1.00	Cr	0.468	Bp	0.112	Zn	0.029
Ze	1.00	Oe	0.394	La	0.096		

The absolute contribution values for each species on axes I and II were calculated (Judez, 1989) and listed in Table 5. Species with absolute contribution value higher than 8.3% (100/12) are indicated in bold. For axis I, these species are (in decreasing order of contribution) *N. hammonis*, *C. lubrica*, *C. aspera*, *A. aculeata*, *Z. excavatus*, and *O. alliarjus*, which together explain 77% of the variance on this axis. For axis II, these species are *A. intermedius*, *O. alliarjus*, *D. rotundatus*, and *C. tridentatum*, which together explain 84% of variance on this axis. We base our interpretation on axis I, since axis II was not significant at the 5% level (Judez, 1989).

According to Figure 3, it can be seen that there is a group of three species (*N. hammonis*, *Z. excavatus*, and *C. lubrica*) which can be clearly differentiated from the rest in relation to their position along the axis. Toward the far right side of this axis, *C. aspera*, *P. pygmaeum*, and *A. aculeata* show a high correlation with this axis, although *A. nitidula* and *V. contracta* also show certain proximity, but with lower contributions to axis I. The two species with lowest absolute contributions to axis I were *C. tridentatum* and *A. intermedius*, which located close to the origin of this axis. *O. alliarjus* shows a higher contribution to axis II than to axis I.

In the plot of sites (Figure 4), most of the woodland sites are located on the right side of axis I, whereas most

Table 2

Eigenvalues, percentage inertias, significance levels, and degrees of freedom for the first four axes extracted by DCA of the 498 \times 47 site-by-species abundance matrix.

Axis	Eigenvalue	% Inertia	χ^2	df
I	0.4018	8.4	< 0.01	491
II	0.2802	5.8	< 0.01	489
III	0.2663	5.6	< 0.05	487
IV	0.2323	4.8	> 0.05	485

Table 3

Coordinates, weights, and absolute contributions to the first two axes extracted by DCA of the 498×47 matrix (see Table 2), for the 18 species whose contribution to at least one of these axes was greater than the average.

Species	Coord. axis I	Coord. axis II	Weight	Contrib. axis I (%)	Contrib. axis II (%)
<i>A. aculeata</i>	-1.7307	0.2755	0.0270	8.0873	0.2049
<i>A. intermedius</i>	0.1809	-0.7525	0.1129	0.3694	6.3930
<i>A. nitidula</i>	-0.6896	0.6063	0.0909	4.3227	3.3414
<i>C. aspera</i>	-1.8361	-0.5628	0.0280	9.4395	0.8868
<i>C. lubrica</i>	0.9731	0.2486	0.1255	11.8838	0.7756
<i>C. barbara</i>	1.3789	2.3641	0.0068	1.2929	3.8004
<i>C. tridentatum</i>	-0.2055	0.7473	0.1030	0.4349	5.7521
<i>D. reticulatum</i>	1.5687	0.7886	0.0150	3.6912	0.9328
<i>D. lombricoides</i>	2.0974	0.1239	0.0052	2.2875	0.0079
<i>D. rotundatus</i>	-0.5257	1.1147	0.0879	2.4292	10.9220
<i>L. cylindracea</i>	-1.3697	-0.1054	0.0126	2.3638	0.0139
<i>N. hammonis</i>	1.0101	-0.9244	0.1497	15.2739	12.7920
<i>O. alliarius</i>	-1.4451	-2.7767	0.0426	8.8962	32.8448
<i>O. elegans</i>	2.6413	5.3712	0.0030	2.0923	8.6549
<i>P. pygmaeum</i>	-1.6918	-0.3795	0.0158	4.5245	0.2275
<i>P. subvirescens</i>	1.4076	0.3170	0.0114	2.2587	0.1145
<i>V. contracta</i>	-1.1475	0.7172	0.0496	6.5311	2.5513
<i>Z. excavatus</i>	0.9669	-0.3249	0.0551	5.1512	0.5816

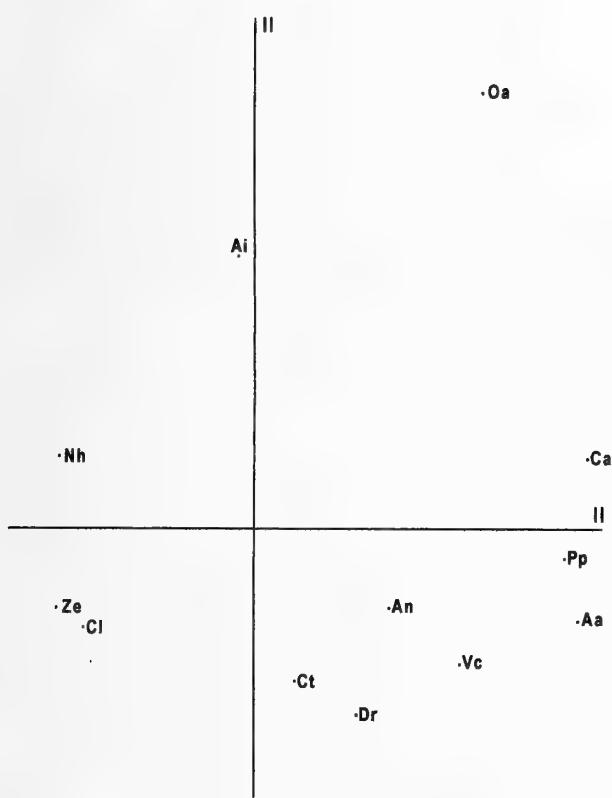


Figure 3

Ordination of the 12 species that were not downweighted on the first two axes extracted by Detrended Correspondence Analysis.

of the meadows are located on the left side. In view of this plot, the woodland gastropod community can be considered to comprise *C. aspera*, *A. aculeata*, *P. pygmaeum*, and *O. alliarius*, accompanied by *V. contracta*, *A. nitidula*, and *D. rotundatus*, while the community of open areas, meadows, comprises *N. hammonis*, *C. lubrica*, and *Z. excavatus*.

To confirm these conclusions, we calculated the centroids. To find out the centroids, a matrix was built in which the variable biotope was converted into a nominal variable. So we assigned to each sample the value 1 or 0, according to their presence or absence into the considered variable. As expected, the woodland centroid lies to the right of the plot, whereas the open-site centroids are plotted to the left (Figure 5). The riverbank centroid lies close to the origin, which is attributable to the fact that such sites represent various biotopes with highly variable characteristics intermediate between woodland and meadow. This heterogeneity of the riverbank sites makes it difficult to discriminate a clearly defined species com-

Table 4

Eigenvalues, percentage inertias, significance levels and degrees of freedom for the first four axes extracted by DCA of the 12 species.

Axis	Eigenvalue	% Inertia	χ^2	df
I	0.388	17.7	< 0.01	440
II	0.287	13.1	> 0.05	438
III	0.220	10.6	> 0.05	436
IV	0.167	7.6	> 0.05	434

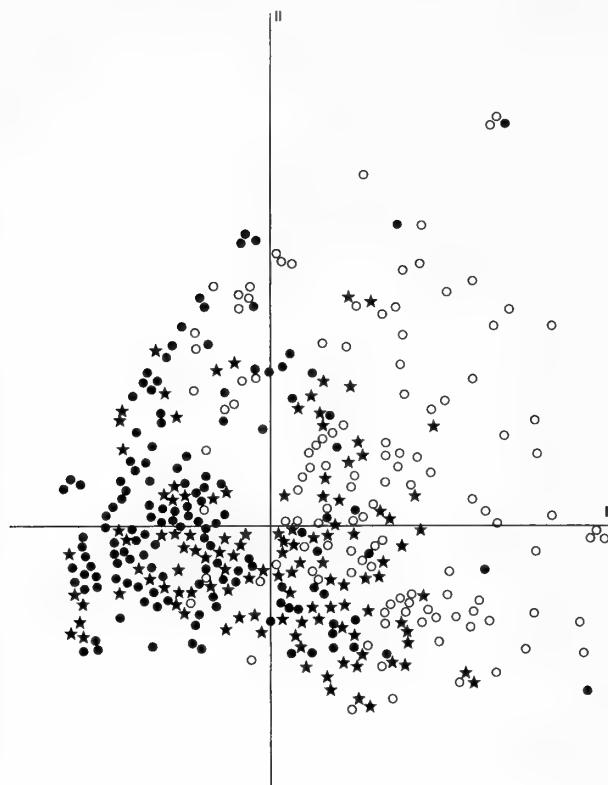


Figure 4

Plot of samples (●, meadow; ★, riverbank; ○, woodland) on the first two axes extracted by DCA of the 12 species.

munity. The characteristic that these riverbank samples have in common is constant moisture supply, which would discriminate aquatic species (not considered in the present study).

Classification

The species-abundance cut-offs selected for definition of pseudospecies for TWINSPAN were 0, 3, 6, 10, 20, 40, and 100, giving up to seven pseudospecies per species. The results of the subsequent classification of sites by pseudospecies are summarized in Figure 6. The first split separated a group (group A) containing most (73%) of the woodland sites, about half (48%) of the riverbank sites, and some (26%) of the meadow sites, from a group (group B) containing most (74%) of the meadow sites, the other half (52%) of the riverbank sites, and some (27%) of the woodland sites.

The results of the classification of species by sites are summarized in Figure 7. The two species groups defined by the first split are very similar to those obtained by DCA: a first group (group A) including *A. aculeata*, *C. aspera*, *O. alliarius*, *P. pygmaeum*, *A. nitidula*, *C. tridentatum*, *V. contracta*, *Euconulus fulvus*, and *Clausilia bi-*



Figure 5

Centroids of the three biotopes (M—meadow; R—riverbank; W—woodland) on the first two axes extracted by DCA of the 12 species.

dentata, and a second group (group B) including *C. lubrica*, *N. hammonis*, *Z. excavatus*, *Deroberas reticulatum*, *Ponentina subvirescens*, *Deroberas lombricoides*, *Deroberas laeve*, and *Vertigo pygmaea*.

The results of classification of sites considering the 12 species used in DCA are summarized in Figure 8. Considering the groups resulting from the first split, the indicator pseudospecies for group A (with abundance class in brackets) are *N. hammonis* (1) and *C. lubrica* (1), while those for group B are *V. contracta* (1), *A. nitidula* (1), and *A. aculeata* (1). Group A contains 79% of woodland sites, 57% of riverbank sites, and 34% of meadow sites, whereas group B contains most meadow sites, somewhat less than half of the riverbank sites, and a small proportion of woodland sites. The first split within group B separates group BB, with indicator pseudospecies *C. lubrica* (2), *C. tridentatum* (1), and *Z. excavatus* (2), containing most of the meadow sites and only a single woodland site, from group BA, containing all other group-B woodland sites. The first split within group A separates group AA, with indicator pseudospecies *C. tridentatum* (1), *A. nitidula* (1), *D. rotundatus* (1), *V. contracta* (1), *C. lubrica* (1), and *A. aculeata* (1), from group AB, with indicator species *O. alliarius* (1).

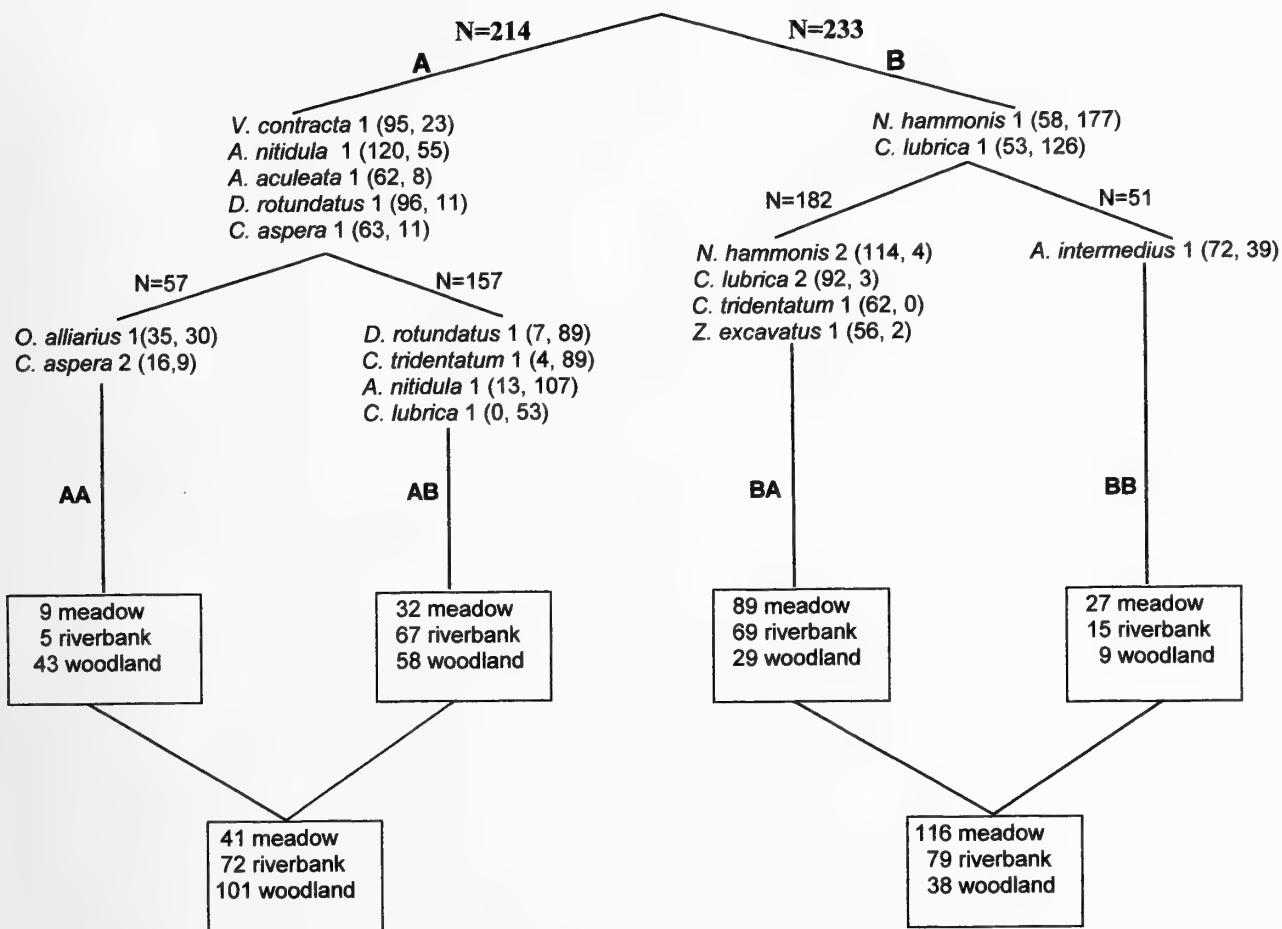


Figure 6

TWINSPAN classification of the samples considering the 47 species, showing the indicator pseudospecies for each split.

The classification of these 12 species by sites (Figure 9) is again very similar to that obtained by DCA. The first split separates a group (group B) comprising *N. hammonis*, *C. lubrica*, and *Z. excavatus* from the rest (group A). The first species to split from group A are *C. tridentatum* and *A. intermedius*, in accordance with the more variable behavior of these taxa (as was indicated by DCA). The remaining species split into two groups: one comprising *V. contracta*, *D. rotundatus*, and *A. nitidula*, the other *P. pygmaeum*, *O. alliarius*, *C. aspera*, and *A. aculeata*.

DISCUSSION

Gastropod populations exist in complex environments reflecting the interaction of numerous factors, including characteristics of the soil-humus-litter-vegetation system. This system is clearly dependent on the herb and woody layers, which contribute to litter formation, filter light,

and buffer variation in moisture levels and temperature. The resulting habitat characteristics are critical for the establishment of certain species, and variations in these factors are the cause of the observed differences among communities.

Taken together, the results of the different analyses indicate that the *C. lubrica*, *N. hammonis*, and *Z. excavatus* characterize the snail communities present in open sites (meadow). The other group comprises *C. aspera*, *O. alliarius*, *A. aculeata*, and *P. pygmaeum*, with preference for wooded areas with more vegetation cover.

V. contracta, *D. rotundatus*, and *A. nitidula* form a group of companion species to the woodland gastropod community, but are also important in riverbank communities, where they are in fact more abundant.

A. intermedius and *C. tridentatum* show more irregular behavior, their presence being more homogeneously distributed, though both appear to have a stronger preference for open areas than for woodland sites.

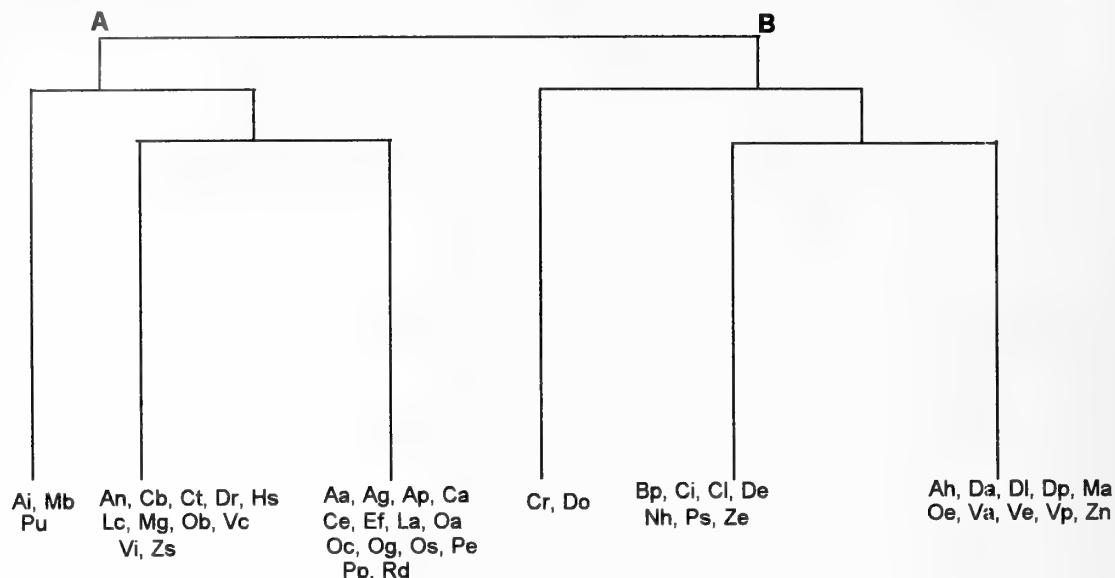


Figure 7
TWINSPAN classification of the 47 species.

Although these are the only species for which statistically significant conclusions may be drawn, in view of their abundances and contribution to the ordination, valid conclusions may also be inferred for a number of other species. Notably, some species that are relatively infrequent in the sample as a whole may in fact be important components of particular habitat types that form subcategories of the major categories (woodland, riverbank, meadow). Species of this type may include the agriolimacids *D. reticulatum*, *D. lombricooides*, and *D. laeve* (which appear to show a preference for open areas), and the group comprising *P. subvirescens*, *Cochlicella barbara*, and *V. pygmaea* (particularly the latter), which is

more abundant in meadow. *E. fulvus*, by contrast, shows a preference for woodland sites.

Some authors, including Boycott (1934), whose study provided the starting point for the majority of more recent studies, have concluded that gastropods show no specific association with vegetation, and that apparent relationships between gastropods and vegetation are due more to environmental conditions than to the fact that the plants in question are food sources (since the variety of the gastropod diet means that this would be a limiting factor only under extreme conditions). Bishop (1977) considered that vegetation has no important effect on the composition of the malacofauna, but that the litter layer (which provides

Table 5

Coordinates, weights, and absolute contributions to the first two axes extracted by DCA for all 12 species included in the analysis.

Species	Coord. axis I	Coord. axis II	Weight	Contrib. axis I (%)	Contrib. axis II (%)
<i>A. aculeata</i>	1.8491	-0.5263	0.0304	10.39	0.84
<i>A. intermedius</i>	-0.1065	1.6338	0.1269	0.14	33.87
<i>A. nitidula</i>	0.7637	-0.4383	0.1022	5.96	1.96
<i>C. aspera</i>	1.9244	0.4041	0.0315	11.66	0.51
<i>C. lubrica</i>	-1.0413	-0.5492	0.1411	15.29	4.25
<i>C. tridentatum</i>	0.1860	-0.8620	0.1163	0.40	8.64
<i>D. rotundatus</i>	0.5363	-1.0580	0.0989	2.84	11.07
<i>N. hammonis</i>	-1.1624	0.4360	0.1683	22.74	3.20
<i>O. alliarium</i>	1.3454	2.5484	0.0479	8.67	31.10
<i>P. pygmaeum</i>	1.7727	-0.1755	0.0177	5.56	0.05
<i>V. contracta</i>	1.1568	-0.7654	0.0558	7.46	3.26
<i>Z. excavatus</i>	-1.1854	-0.4309	0.0620	8.71	1.15

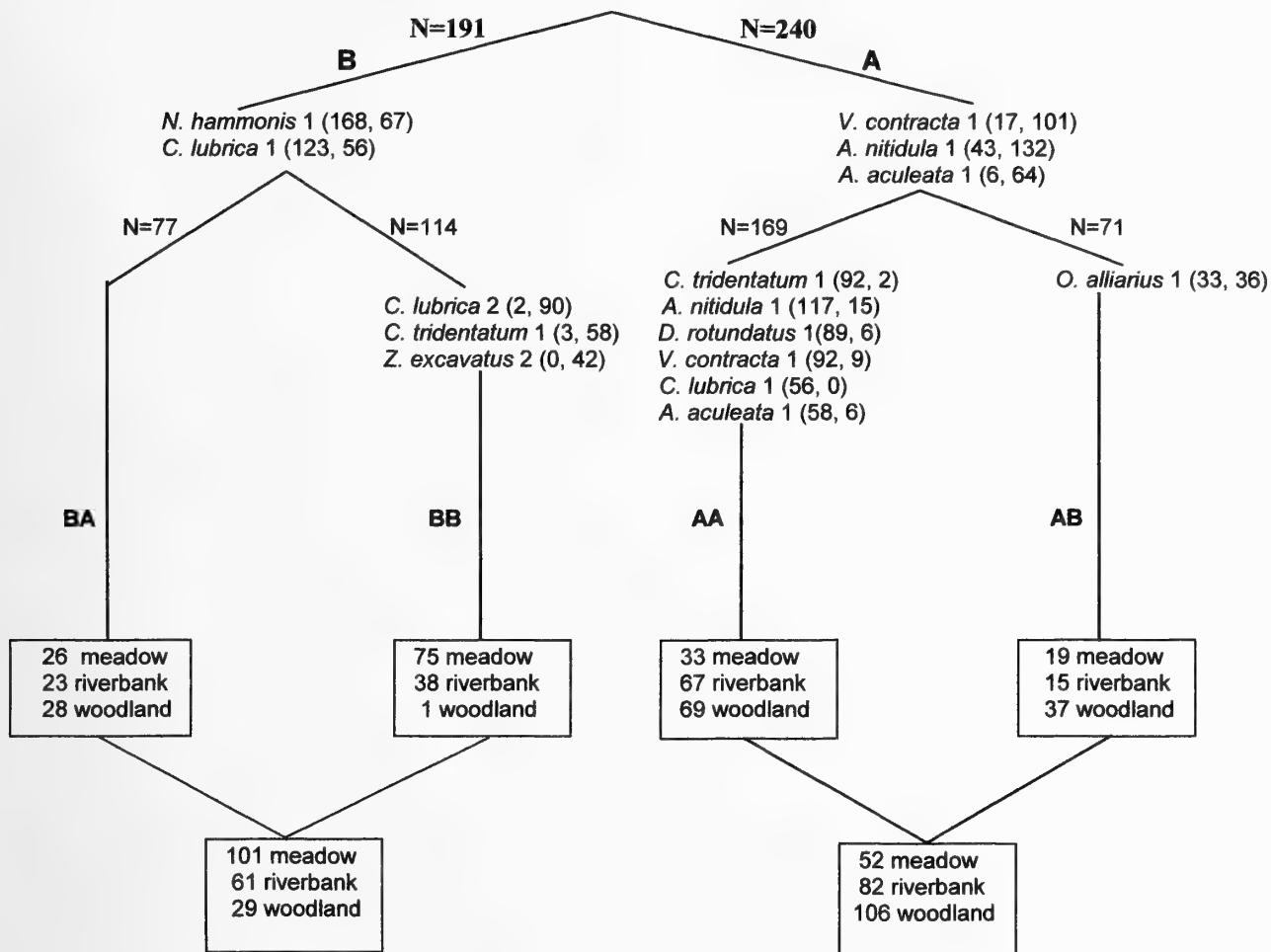


Figure 8

TWINSPAN classification of the samples, considering the 12 species considered in the second DCA.

food and shelter) has a marked effect, important factors being mineral content, surface bacterial and fungal populations, and the amount of usable litter. Locasciulli & Boag (1987) pointed out that litter layer characteristics depend on the overlying vegetation, and took as their starting point the assumption that gastropods do not use the litter layer directly, but rather nutrients derived from it; nevertheless, they stressed the importance of the litter layer for providing a stable microclimate.

In the present study, we have taken as our starting point the view that even the most common and most euryecious species do not occur in all vegetation types; all species prefer some biotopes over others, so that different biotopes can be considered rich or poor depending on the conditions that they offer to the specific demands of the species in question. Thus each biotope may contain characteristic associations, and it is thus probably the condi-

tions created by that biotope that determine the establishment of the malacofauna.

Woodland vegetation may itself provide the gastropod fauna with the necessary conditions for survival: it buffers variations in temperature and humidity, and provides shelter and varied microhabitats such as tree roots, fallen trunks, hollows, together with a usable humus and litter layer. The tree cover performs a basic microclimatic role, which is probably more important than the composition of the litter layer. It is indeed the presence or absence of climate-buffering tree cover that largely explains the difference in malacofauna between woodland and meadow biotopes: the latter are exposed to marked daily and seasonal variations in temperature, humidity, and light intensity (Dillon, 1980; Boag & Wishart, 1982; Curry, 1994). Species that occur preferentially in meadow are probably more resistant to such variation, and escape its effects by

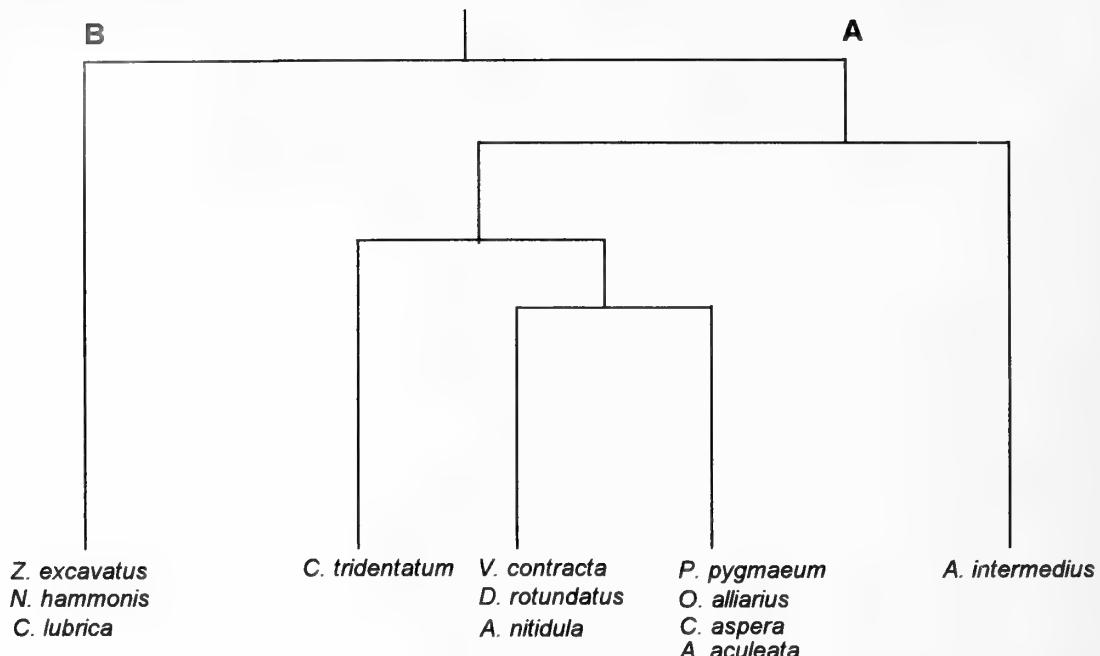


Figure 9

TWINSPAN classification of the 12 species considered in the second DCA.

burrowing into the soil (Stephenson, 1966 in Peake, 1978; Outeiro et al., 1989; Outeiro et al., 1993), or are more influenced by other non-microclimatic factors first, such as biotope factors, or soil factors, or factors not considered in the present study, such as the quality of the litter or the herb layer.

Riverbanks constitute such a heterogeneous category that fauna of both types are present, especially species at the limits of the requirements of the other biotopes. These habitats thus probably behave as ecotones, as well as being favorable because of water availability.

In order to facilitate comparison of our results with those of previous studies, we have summarized previous results in Table 6. Like us, most authors have reported *C. lubrica* and *N. hammonis* to be species of meadow, though only Riballo (1990) also included *Z. excavatus* as the third characteristic species of this community. Previous reports of species characteristic of woodland communities, however, show some discrepancies. For example, Alonso (1977) concluded that *C. lubrica* is characteristic of poplar groves. This is probably attributable to the particular characteristics of poplar groves, in which trees are planted in existing meadow, where *C. lubrica* was probably already present.

Bába (1981) likewise considered *C. lubrica* to be a constant species within the malacofauna of woodland sites. This author's aim was to identify relationships between the successional series of gastropod communities and plant communities along a river. The only habitats

considered were woodland biotopes, characterized by various moisture and temperature indices; there was thus no comparison with other biotopes. Similar conclusions were reached by Wäreborn (1982), who considered *N. hammonis* and *C. lubrica* to be characteristic of woodland (again the only biotope considered), though it should be stressed that the characterization of biotopes in terms of malacofauna was not one of the goals of this study, so that there was no comparison with other biotopes. This author also found that *C. lubrica* may occur at high abundance in meadow. Waldén (1955) reported that *C. lubrica* is a species typical of woodlands, but this conclusion was not based on a uniform sampling strategy (16 samples were obtained from woodland sites, versus only four from open sites). This author likewise reported that *C. lubrica* may be abundant in swamps and marshes. Note, however, that Waldén's data analysis (using percentage abundances) is not directly comparable with that used in the present study.

The few previous studies to consider *Z. excavatus* have concluded that it is a woodland species (Boycott, 1934; Bishop, 1977; Anderson, 1983); this contrasts with the present study, and with Riballo (1990), who found that *Z. excavatus* appears to be characteristic of meadow. Riballo (1990) states that the distribution of *Z. excavatus* is wider than has been suggested by some previous authors; indeed, Anderson (1983) also found this species in meadow, and remarked that in acid soils (as in the present study) it typically occurs in association with *N. hammon-*

Table 6

Summarized findings of previous studies for the 12 species considered showing whether each species is judged to be characteristic of meadow (♣), characteristic of woodland (●), or ubiquitous (♦).

Authors	CI	Nh	Ze	Ca	Oa	Aa	Pp	Vc	An	Dr	Ct	Ai
Alonso, 1977	●						●				●	
Anderson, 1983			●	●	●	●	●					
André, 1982	♣				●	●	●	●		●		
Bába, 1981	●	●					●	●				
Badie & Rondelaud, 1979	♣	♣										
Bishop, 1977	●		●	●	●	●	●		●	●		●
Boycott, 1934		●			●	●	●		●	●		
Cameron, 1973, 1978					●			●	●			♦
Cameron et al. 1980					●	●	●			●		
Frank, 1979	♣	♣				●	●			●	●	
Hermida et al., 1994	♣	♣			●	●	●	●	●			♦
Jourdin et al., 1985	♣											
Kornig, 1989	♣	♣										
Mason, 1974					●	●	●	●	●	●	●	
Matzke, 1976	♣											
Meier, 1987	♣	♣										
Mordan, 1977	♣											
Ojea & Anadón, 1983	♣							●				
Ojea et al., 1987	♣	♣				●	●	●	♦	●	♦	♦
Outeiro, 1988	♣	♣				●	●	●		●	♦	♦
Outeiro et al., 1989							●					
Paul, 1975a,b				●		●			●	●	●	
Paul, 1978a,b	♦					●	●		●	●	●	
Phillipson & Abel, 1983						●	●	●		●		
Radea & Mylonas, 1992						●	●					
Riballo, 1990	♣	♣	♣	●		●	●	●	●	●		♦
Riballo et al., 1995						●	●	●	●	●	●	
Solhöy, 1981	♣	♣					●			●		♦
South, 1992						●	●	●				♦
Štamol, 1993												
Tattersfield, 1990												♦
Valovirta, 1967, 1979			●	●	●	●	●		●			
Waldén, 1955	●					●	●	●				
Wäreborn, 1982	●	●				●			●	●	●	

is. Boycott (1934) did not find this species in his woodland sites and, although he referred to it as a woodland taxon, he stated that its special characteristics (notably calciphobia and sensitivity to competition) lead it to live "where it can" and not "where it would like to." In any case, there have been few ecological studies of this species, and there is a shortage of data to facilitate statistical investigation of putative relationships with particular types of biotope.

Our results for both *P. pygmaeum* and *A. aculeata* agree closely with previous reports; both have consistently been identified as woodland species. Similarly, our results for *C. aspera* and *O. alliarius*, classified in the present study as characteristic of woodland, likewise show close agreement with previous studies. The species classified in the present study as woodland-community companion species have often been described as woodland species, supporting our findings.

The present results indicate that *C. tridentatum* and *A. intermedius* should be considered as ubiquitous species, whereas some previous studies have classified these species as characteristic of woodland. This difference is probably attributable to the fact that these previous studies considered only woodland sites, therefore the presence in this biotope of ubiquitous species seems logical. Moreover, some of the species classified in the present study as characteristic of meadow or riverbank have previously been classified as ubiquitous by previous authors.

It should be borne in mind that there have been few studies in which the sampling method or the statistical treatment of the data have been directly comparable with those used in the present study. Furthermore, most previous studies included consideration of species that are absent from our region, or that did not show significant habitat preferences in the present study. André (1982) studied terrestrial mollusk populations in *Quercus pubes-*

cens communities, and by means of multivariate analysis techniques obtained an ordination of samples and species that is very similar to that obtained in the present study. He likewise characterized two contrasting groups of samples, on the one hand samples from open sites, and on the other, samples from sites with taller vegetation cover. Many of the species present in this author's samples were not present in our samples. Nevertheless, our results for those species present in both studies show close agreement, with *C. lubrica* characteristic of open sites, and *D. rotundatus*, *E. fulvus*, *A. aculeata*, and *P. pygmaeum* characteristic of woodland or semi-woodland sites.

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APPENDIX I

List of species detected in the present study, in each case showing species code (e.g., **Aa**), species name and authority, and total number of individuals detected.

- Aa:** *Acanthinula aculeata* (Müller, 1774) (191)
- Ag:** *Azeca goodalli* (A. Féruccac, 1821) (30)
- Ah:** *Arion hortensis* A. Féruccac, 1819 (9)
- Ai:** *Arion intermedius* Normand, 1852 (1220)
- An:** *Aegopinella nitidula* (Draparnaud, 1805) (1024)
- Ap:** *Aegopinella pura* (Alder, 1830) (4)
- Bp:** *Balea perversa* (Linnaeus, 1758) (5)
- Ca:** *Columella aspera* Waldén, 1966 (175)
- Cb:** *Clausilia bidentata* (Ström, 1765) (121)
- Ce:** *Columella edentula* (Draparnaud, 1805) (3)
- Ci:** *Candidula intersecta* (Poiret, 1801) (15)
- Cl:** *Cionella lubrica* (Müller, 1774) (3167)
- Cr:** *Cochlicella barbara* (Linnaeus, 1758) (395)
- Ct:** *Carychium tridentatum* (Risso, 1826) (2713)
- Da:** *Deroceras agreste* (Linnaeus, 1758) (2)
- De:** *Deroceras reticulatum* (Müller, 1774) (108)
- Dl:** *Deroceras laeve* (Müller, 1774) (42)
- Do:** *Deroceras lombricoides* (Morelet, 1845) (63)
- Dp:** *Deroceras panormitanum* (Lessona & Pollonera, 1882) (1)
- Dr:** *Discus rotundatus* (Müller, 1774) (1723)
- Ef:** *Euconulus fulvus* (Müller, 1774) (84)
- Hs:** *Helicodiscus* sp. Morse, 1864 (81)
- La:** *Leiostyla anglica* (Wood, 1828) (49)
- Lc:** *Lauria cylindracea* (Da Costa, 1778) (560)
- Ma:** *Milax gagates* (Draparnaud, 1801) (8)
- Mb:** *Mengoana brigantina* (Da Silva, 1867) (2)
- Mg:** *Ashfordia granulata* (Alder, 1830) (43)
- Nh:** *Nesovitreahammonis* (Ström, 1765) (3223)
- Oa:** *Oxychilus alliarius* (Miller, 1822) (371)
- Ob:** *Oestophora barbula* (Rossmässler, 1838) (81)
- Oc:** *Oxychilus cellarius* (Müller, 1774) (29)
- Oe:** *Oxyloma elegans* (Risso, 1826) (80)
- Og:** *Oxychilus glaber* (Rossmässler, 1835) (15)
- Os:** *Oestophora silvae* Ortiz de Zárate, 1962 (32)
- Pe:** *Pomatias elegans* (Müller, 1774) (1)
- Ps:** *Ponentina subvirescens* (Bellamy, 1839) (208)
- Pp:** *Punctum pygmaeum* (Draparnaud, 1801) (95)
- Rd:** *Rumina decollata* (Linnaeus, 1758) (20)
- Pu:** *Paralaoma caputspinulae* (Reeve, 1852) (33)
- Va:** *Vertigo antivertigo* (Draparnaud, 1801) (3)
- Vc:** *Vitrea contracta* (Westerlund, 1871) (391)
- Ve:** *Vallonia excentrica* Sterki, 1892 (364)
- Vi:** *Vitrina pellucida* (Müller, 1774) (9)
- Vp:** *Vertigo pygmaea* (Draparnaud, 1801) (77)
- Ze:** *Zonitoides excavatus* (Alder, 1830) (1024)
- Zn:** *Zonitoides nitidus* (Müller, 1774) (1)
- Zs:** *Zenobiella subrufescens* (Miller, 1822) (17)

Total 17,902

The Subgenus *Lentigo* (Gastropoda: Strombidae) in Tropical America, Fossil and Living

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Abstract. The hitherto unknown occurrence of the strombid subgenus *Lentigo* in deposits of Neogene and Quaternary age in tropical America is documented. Sixteen species are recognized, which occur at 17 different general locations throughout the Caribbean. The oldest record is from the early middle Miocene of Carriacou, Lesser Antilles, and the youngest from the Holocene of Isla Margarita, Venezuela. *Lentigo* is therefore documented over a time interval of about 15 million years. Four species are described as new: *S. barrigonensis* from the Cubagua Formation (early Pliocene) of the Araya Peninsula, Venezuela; *S. toroensis* from the Cayo Agua Formation (early Pliocene) of Cayo Agua, Bocas del Toro, Panama; *S. fetus* from the Escudo de Veraguas Formation (late Pliocene) of Escudo de Veraguas, Bocas del Toro, Panama; and *S. insulanus* from the Escudo de Veraguas Formation (middle Pliocene part) of Escudo de Veraguas.

INTRODUCTION

While making up faunal lists of assemblages from the island of Escudo de Veraguas, Bocas del Toro, Panama for the Panama Paleontology Project (PPP), the senior author came across a small incomplete specimen of some kind of *Strombus* he thought he had never seen before. The puzzling feature of this specimen was three spiral rows of knobs on the dorsal side of the body whorl. He showed the specimen to the junior author, who almost immediately said that he remembered an article in a French journal dealing with species of *Strombus* showing that very feature: it was the paper by Lozouet & Maestrati (1986). In that paper the authors discussed two species of the subgenus *Lentigo*, Jousseaume, 1886, from the European late Eocene and Oligocene to early Miocene, respectively, stating that the late Eocene species must have given rise to the living Eastern Pacific *Strombus granulatus*, Swainson, 1822, since no species of *Lentigo* was known from the American Cenozoic. We could hardly believe this statement, and we decided to search the collections of the Basel Natural History Museum, old collections and the new PPP collections. The result was astonishing: we found a total of 43 fossil specimens of *Lentigo*, 26 in the old collections, and 17 in the new PPP collections. This admittedly not very rich material is here assigned to 16 “species.” The word species is put in quotation marks because five of them are identified by letters only, six are positively identified, and five are identified by means of open nomenclature. Some of these “species” are represented by a single more or less well-preserved specimen or even by a fragment only. In case additional material should become available in the future, the number of species or their designation may have to be modified.

The purpose of this paper is to document the occurrences of species of the subgenus *Lentigo* in the Neogene and Quaternary of tropical America. It is not the purpose to give a revision of the subgenus.

As now understood, the subgenus *Lentigo* seems to be characterized by two features. First: *Lentigo* has three or four axial swellings per whorl on the earliest teleoconch whorls with a varying number of axial ribs in the interspaces. On succeeding whorls the axial sculptural elements become subequal in size. Second: *Lentigo* has two or more spiral rows of knobs on the dorsal side of the body whorl.

We are aware that this is not a convincing definition of the subgenus, but this goes for other subgenera of *Strombus* as well. As a matter of fact, the family Strombidae badly needs a thorough revision. We know very little about the ontogenetic development of strombid species. Careful studies of protoconchs and the sculptural development of early teleoconch whorls should be undertaken. Such studies will at the same time help the understanding of variability in strombid species. However, for the time being we are in the dark and are perhaps guessing too much.

Abbreviations

The following abbreviations are used for repository institutions and field numbers: AM, Australian Museum, Sydney; ANSP, Academy of Natural Sciences, Philadelphia, Pennsylvania, USA; BMNH, British Museum (Natural History), now The Natural History Museum London; CJ, Coates/Jackson localities; FMNH, Field Museum of Natural History, Chicago, Illinois, USA; GS, Gibson-Smith localities; LACM, Los Angeles County Museum of Natural History, Los Angeles, California, USA; NMB, Na-

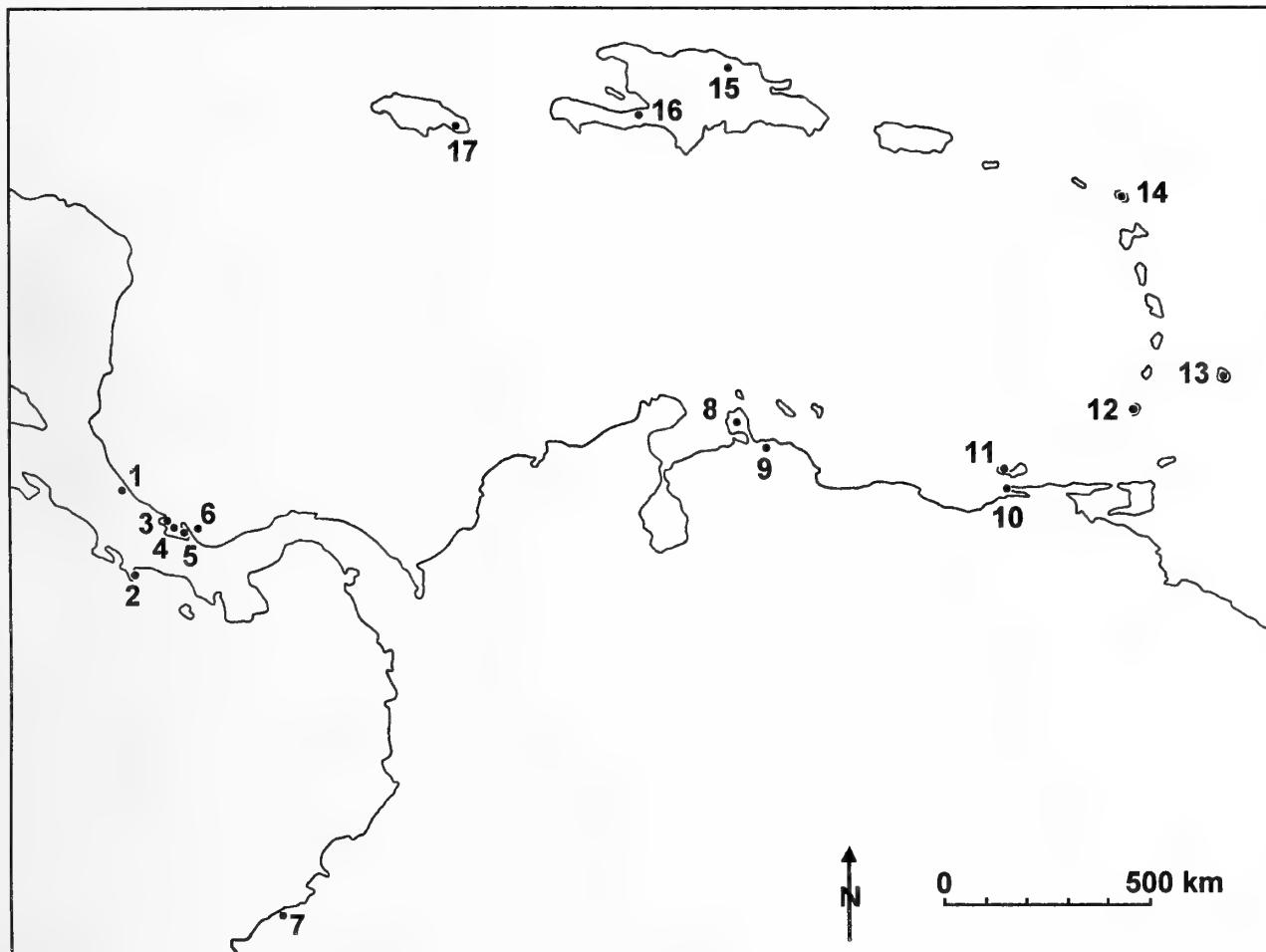


Figure 1. Fossil occurrences of the subgenus *Lentigo* in tropical America. The numbers are arranged anticlockwise (for ages see Table 1). 1. Limón, Costa Rica: *S. cf. raninus*. 2. Burica Peninsula, Panama: *S. granulatus* and *S. sp. D*. 3. Isla Colón, Panama: *S. cf. granulatus* and *S. raninus*. 4. Cayo Agua, Panama: *S. cf. fetus* Jung & Heitz, sp.nov. *S. toroensis* Jung & Heitz, sp.nov. 5. Valiente Peninsula, Panama: *S. sp. B*. 6. Escudo de Veraguas, Panama: *S. fetus* Jung & Heitz, sp.nov. and *S. insulanus* Jung & Heitz, sp.nov. 7. About 1 km west of Camarones, Esmeraldas Province, Ecuador: *S. granulatus*. 8. Paraguaná Peninsula, Falcón, Venezuela: *S. sp. C*. 9. Carrizal, Falcón, Venezuela: *S. sp. A*. 10. Araya Peninsula, Sucre, Venezuela: *S. barrigonensis* Jung & Heitz, sp.nov. 11. Isla Margarita, Nueva Esparta, Venezuela: *S. raninus*. 12. Carriacou, Grenadines, Lesser Antilles: *S. cf. insulanus* Jung & Heitz, sp.nov. 13. Barbados: *S. raninus*. 14. Antigua, Lesser Antilles: *S. raninus*. 15. Santiago, Dominican Republic: *S. aff. raninus*. 16. Port-au-Prince, Haiti: *S. raninus*. 17. Bowden, Port Morant, Jamaica: *S. sp. E*.

turhistorisches Museum Basel; PJ, Peter Jung localities; PPP, Panama Paleontology Project; USNM, National Museum of Natural History, Washington, D.C., USA.

DISTRIBUTION THROUGH TIME AND SPACE

When discussing the living Indo-Pacific species of *Lentigo*, Abbott (1960:117) also assigned *Strombus aldrichi* Dall (1890:175, pl. 12, figs. 1, 4) from the early Miocene Chipola Formation of Florida to that subgenus. Lozouet & Maestrati (1986:15) disagreed with that assignment by simply stating that *S. aldrichi* is a species very different from the “*radix-granulatus* group.”

If we presume for a moment that *S. aldrichi* actually

is a member of the subgenus *Lentigo*, it represents not only the oldest but also a rather isolated occurrence in the Western Hemisphere. In the original description of *S. aldrichi* Dall (1890:176) expressed the opinion that it was related to the living *S. granulatus*.

Strombus aldrichi is indeed a problem. We have eight specimens from the Chipola Formation of Florida at hand. In general shape they are similar to the material reported on herein, but their relationship to that material is not clear. As in other species of *Lentigo*, the early teleoconch whorls of *S. aldrichi* are sculptured by three axial swellings per whorl and four to eight axial ribs in the interspaces, all of which are crossed by spiral threads. On the



Figure 2. *Strombus (Lentigo) lentiginosus* Linnaeus. A-C. LACM 79-42.2. Intertidal - 2 m, dead coral, Korolevu, Viti Levu, Fiji ($18^{\circ} 13.2'S$, $177^{\circ} 43.1'E$). Height 75.3 mm, width 47.0 mm. A. Front view. B. Rear view. C. From right side. $\times 1.5$.

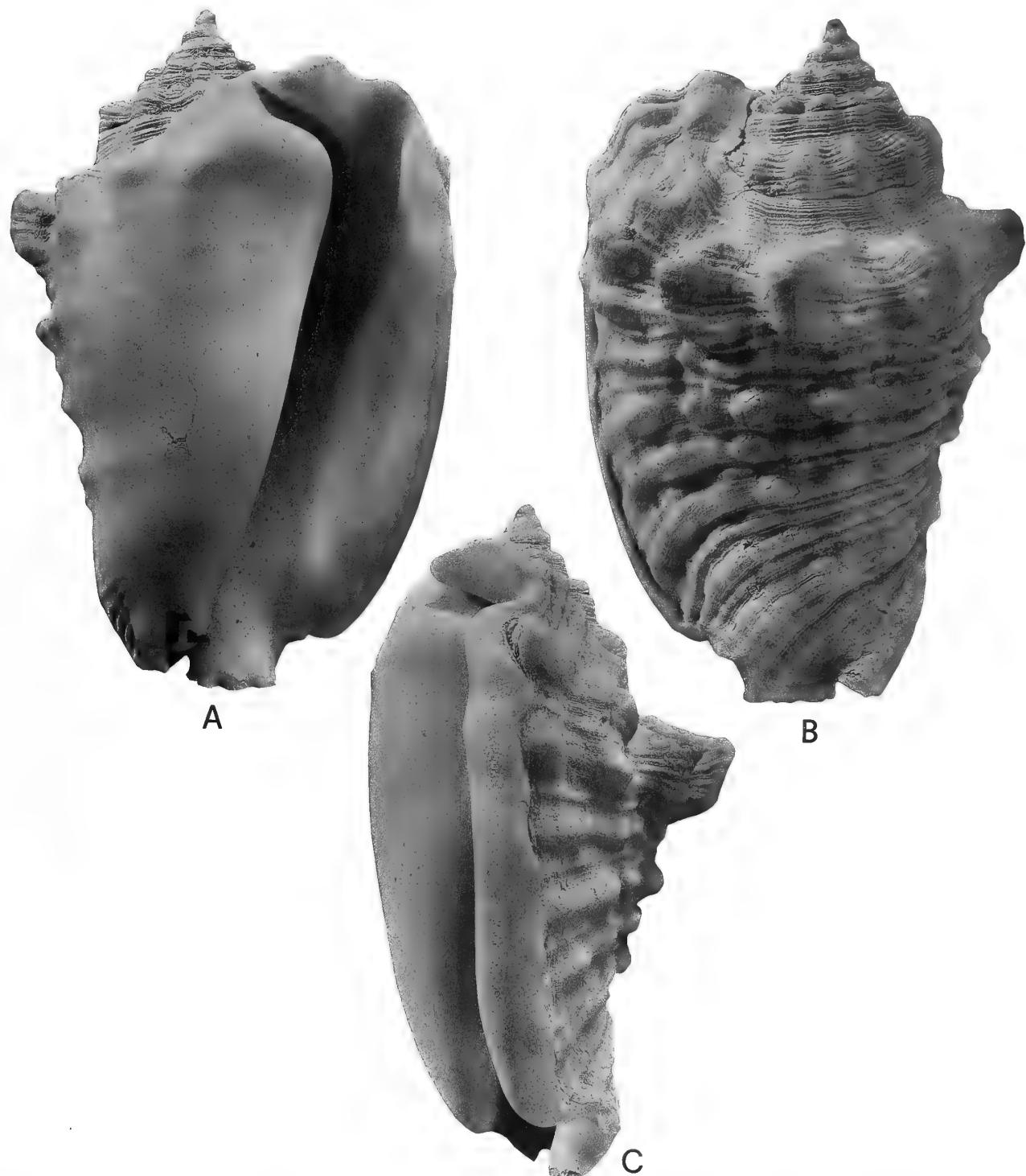


Figure 3. *Strombus (Lentigo) lentiginosus* Linnaeus. A–C. LACM 72-138.2. Beach shells, Seychelles (5°S , 56°E). Height 75.0 mm, width 50.4 mm. A. Front view. B. Rear view. C. From right side. Comparing with Figure 2 note variability in spiral ribbing on dorsal surface of shell. $\times 1.5$.

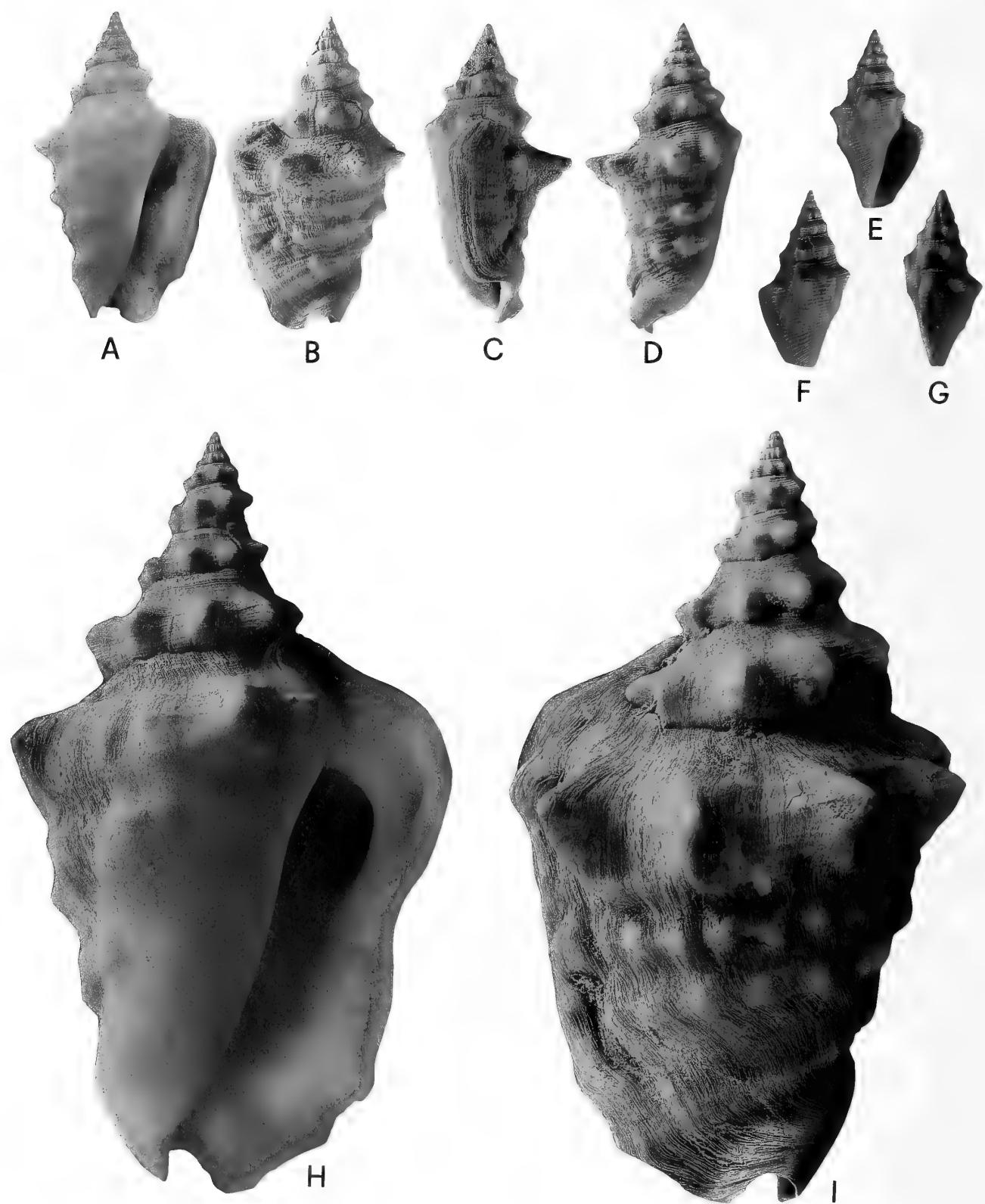


Table 1
Summary of stratigraphic occurrences of species of the subgenus *Lentigo*.

Species	Locality	Formation, Member	Age	Absolute Age in My
<i>S. granulatus</i>	Burica Peninsula, Panama near Esmeraldas, Ecuador	Armuelles Fm. upper Onzole Fm.	Pleistocene late Pliocene	0.45
<i>S. cf. granulatus</i>	Isla Colón, Panama	unnamed	Plio-Pleistocene	1.7–3.5
<i>S. raninus</i>	1. Isla Colón, Panama 2. Isla Margarita, Venezuela 3. Barbados 4. Antigua 5. Port-au-Prince, Haiti	1. unnamed 2. Boca Chica Fm. 3. unnamed 4. unnamed 5. unnamed	1. Plio-Pleistocene 2. Holocene 3. Pleistocene 4. Holocene 5. Pleistocene	1.7–3.5
<i>S. aff. raninus</i>	Santiago, Dominican Republic	Gurabo Fm.	early Pliocene	
<i>S. cf. raninus</i>	Limón, Costa Rica	Moín Fm.	Plio-Pleistocene	1.5–1.9
<i>S. barrigonensis</i>	Araya Peninsula, Venezuela	Cubagua Fm., Cerro Negro Mb.	early Pliocene	
<i>S. toroensis</i>	Cayo Agua, Panama	Cayo Agua Fm.	early Pliocene	4–5
<i>S. fetus</i>	Escudo de Veraguas	Escudo de Veraguas Fm.	late Pliocene	1.9–2.2
<i>S. cf. fetus</i>	Cayo Agua, Panama	Cayo Agua Fm.	middle Pliocene	3.5–3.6
<i>S. insulanus</i>	Escudo de Veraguas	Escudo de Veraguas Fm.	middle Pliocene	3.5–3.6
<i>S. cf. insulanus</i>	Carriacou, Grenadines	Grand Bay Fm.	early middle Miocene	
<i>S. sp. A</i>	Carrizal, Falcón, Venezuela	Caujara Fm., Mataruca Mb.	late Miocene	
<i>S. sp. B</i>	Valiente Peninsula, Panama	Shark Hole Point Fm.	Pliocene	
<i>S. sp. C</i>	Paraguaná, Falcón, Venezuela	El Porvenir beds	middle/late Miocene	
<i>S. sp. D</i>	Burica Peninsula, Panama	Armuelles Fm.	Pleistocene	0.45
<i>S. sp. E</i>	Bowden, Jamaica	Bowden Fm.	early Pliocene	

other hand, *S. aldrichi* lacks the other characteristic feature of *Lentigo*: the spiral rows of knobs on the dorsal side of the body whorl. If *S. aldrichi* belongs to *Lentigo*, its distant ancestor must be one of the European species discussed by Lozouet & Maestrati (1986). One of the unknown ancestors of *S. aldrichi* must have lost (or never had) the characteristic feature of spiral rows of knobs on the dorsal side of the body whorl, which has not been reacquired since.

The 16 species recognized in this paper occur at 17 different general locations (Figure 1). The westernmost location is situated west of Limón, Costa Rica. The northernmost location is Santiago, Dominican Republic; the easternmost locality is Barbados, Lesser Antilles; and the southernmost occurrence is the Esmeraldas Province, Ecuador. In other words, the subgenus *Lentigo* is spread over a large area mostly covered by water with a north-south extension of about 2000 km and an east-west extension of about 2500 km. The part of the Pacific Ocean

shown in Figure 1 is inhabited by *S. granulatus* and that of the Caribbean Sea by *S. raninus*.

The stratigraphic occurrences of the 16 species are listed in Table 1. The oldest record is *Strombus (Lentigo) cf. insulanus* n. sp. from the early middle Miocene Grand Bay Formation of Carriacou, and the youngest record is the single specimen of *S. raninus* from the Holocene Boca Chica Formation of Isla Margarita, Venezuela. The material described in this paper therefore covers a time interval of about 15 my.

SYSTEMATIC DESCRIPTIONS

Genus *Strombus* Linnaeus

Linnaeus, 1758:742.

Type species: (by subsequent designation, Montfort, 1810: 515)—*Strombus pugilis* Linnaeus, 1758:744. Recent, West Indies and Florida.

←

Figure 4. *Strombus (Lentigo) granulatus* Swainson. A–D. LACM 39-62.6. 4–9 m, mud and sand, Isla Taboga, Panama ($8^{\circ} 48'N$, $79^{\circ}30'W$). Height 37.2 mm, width 22.4 mm. A. Front view. B. Rear view. C. From right side. D. From left side. E–G. LACM 33-121.4. Shallow water, Bahía Honda, Veraguas Prov., Panama ($7^{\circ}43.77'N$, $81^{\circ}31.90'W$). Height 21.2 mm, width 11.6 mm. E. Front view; F. Rear view G. From right side. Note that only one spiral row of knobs below the periphery is developed in this immature specimen. H–I: LACM 66-28.5. Low intertidal – 1.8 m, Bahía Partida, between Isla Partida and Isla Espíritu Santo, Gulf of California, Baja California Sur, Mexico ($24^{\circ} 31'N$, $110^{\circ} 23'W$). Height 92.6 mm, width 56.7 mm. H. Front view. I. Rear view. All $\times 1.5$.



Figure 5. *Strombus (Lentigo) granulatus* Swainson. LACM 66-28.5. A-B. Same specimen as Figure 4H and 4I. A. From right side. B. From left side. $\times 1.5$.

Subgenus *Lentigo* Jousseaume

Jousseaume, 1886:220.

Type species: (by monotypy) *Lentigo lentiginosus* Linnaeus, 1758:743. Recent. East Africa to the Marshall and Tuamotu Islands according to Abbott (1960:117).

Remarks: It is not the purpose of this paper to review the subgenus *Lentigo*, but to document its occurrence in tropical America. A proper review of *Lentigo* would require the study of much more material and from a broader geographic area. For this reason, we refrain from the attempt to give a proper diagnosis of the subgenus. However, there seem to be two features that largely define *Lentigo*. First: *Lentigo* has three or four axial swellings per whorl on the earliest teleoconch whorls with a varying number of axial ribs in the interspaces. Second: *Lentigo* has two or more spiral rows of knobs on the dorsal

side of the body whorl. Future work on the group may reveal additional diagnostic characters.

Among the species recorded herein the first feature is seen in *S. granulatus*, *S. raninus*, and *S. insulanus*. In *S. barrigonensis* and *S. fetus* it is not documented because the earliest teleoconch whorls are not preserved. Their assignment to *Lentigo* is therefore mainly based on the second feature.

Species like *Strombus pugilis* Linnaeus, 1758, and *S. alatus* Gmelin, 1791, which are assigned to the subgenus *Strombus*, or *S. gigas* Linnaeus, 1758, and *S. costatus* Gmelin, 1791, which are members of the subgenus *Tricornis* Jousseaume, 1886, all have no axial swellings on the earliest teleoconch whorls, but axial ribs of about the same size.

The stratigraphic range of *Lentigo* is late Eocene to Recent.

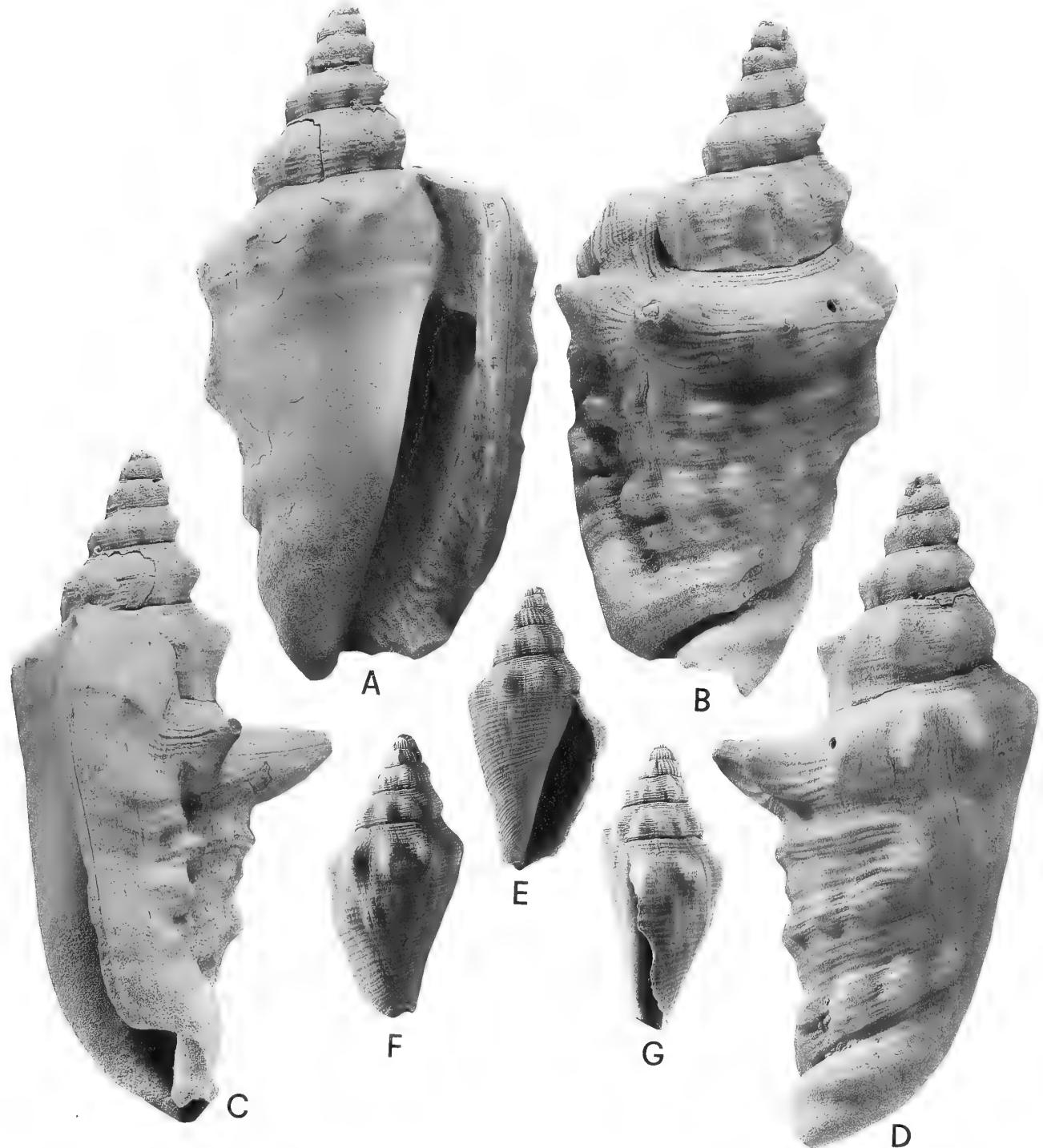


Figure 6. *Strombus (Lentigo) granulatus* Swainson. A-D. NMB H 17844. NMB locality 18419 (= CJ-87-04-37 = PPP 00144); east coast of Burica Peninsula, Panama; 100 m S of Boca Quebrada Corotú. Armuelles Formation (Pleistocene). Height 75.2 mm, width 40.1 mm. A. Front view. B. Rear view. C. From right side. D. From left side. E-G. NMB H 17843. NMB locality 17439; east coast of Burica Peninsula, Panama; 400 m S of Boca Quebrada Corotú. Armuelles Formation (Pleistocene). Height 31.9 mm, width 16.6 mm. E. Front view. F. Rear view. G. From right side. Note that the spiral row of knobs below the periphery is only weakly developed (compare with Figure 4E-G). Both specimens $\times 1.5$.

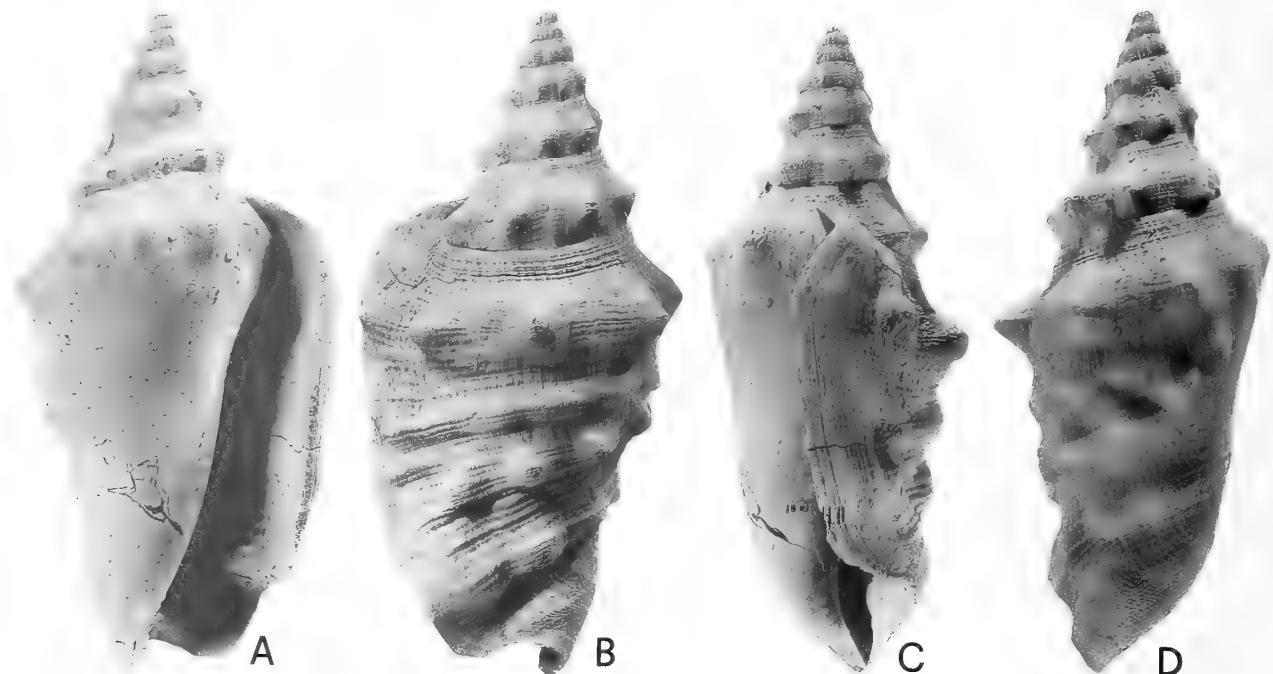


Figure 7. *Strombus (Lentigo) granulatus* Swainson. A–D. BMNH PI TG 4731: road-cutting about 1 km west of village of Camarones, Esmeraldas Province, Ecuador. Upper Onzole Formation (late Pliocene) (for general location see number 7 of Figure 1). Height 58.4 mm, width 29.0 mm. A. Front view. B. Rear view. C. From right side. D. From left side. $\times 1.5$.

Strombus (Lentigo) lentiginosus Linnaeus
(Figures 2, 3)

Strombus lentiginosus Linnaeus, 1758:743.

Strombus (Lentigo) lentiginosus Linnaeus, Abbott, 1960: 117, pl. 17, figs. 11, 12; pl. 94, fig. 4. For additional citations see this publication. Lozouet & Maestrati, 1986:12, fig. (unnumbered).

Remarks: We have received two specimens of this species on loan from the Los Angeles County Museum of Natural History. One specimen is from the Seychelles (LACM 72-138.2), the other from Korolevu, Viti Levu, Fiji (LACM 79-42.2). Both are illustrated here for comparison with a fossil specimen from the island of Escudo de Veraguas, Bocas del Toro, Panama (see under *Strombus (Lentigo) fetus* n. sp.).

Depth range and substratum: From low tide mark to about 12 feet, usually on a coral sand bottom which may be rocky and with weeds (Abbott, 1960:117).

Geographic distribution: From East Africa to the Marshall and Tuamotu Islands (Abbott, 1960:117, pl. 96).

Strombus (Lentigo) granulatus Swainson
(Figures 4–10)

Strombus granulatus Swainson, 1822:43, and Appendix, p. 8.
Strombus (Lentigo) granulatus Swainson, 1822, Emerson &

Old, 1963:7, figs. 4, 6–8 (for additional citations see this publication), Keen, 1971:421, fig. 608. Abbott, 1974:144, color plate 4, fig. 1582. Lozouet & Maestrati, 1986:11, 12, figs. A–D.

Strombus granulatus Mawe, 1823:125, 127, pl. 25, fig. 3. Grant & Gale, 1931:755 (for additional citations see this publication). Durham, 1950:117, pl. 27, figs. 3, 8.

Strombus granulatus acutus Durham, 1950:118, pl. 27, figs. 1, 2, 5 (not Perry, 1811, pl. 12, fig. 2). *Strombus granulatus cortezianus* Durham, 1962:213.

Description: Shell reaching a height of about 90 mm, moderately slender. Protoconch with five rapidly enlarging smooth volutions. Profile of first three volutions flat, of fourth and fifth volution, convex. On second third volution of protoconch there is an indication of a spiral ornamentation near abapical suture. Dividing line between protoconch and teleoconch slightly opisthocyst. Number of teleoconch whorls up to about eight. Initial sculpture of teleoconch consists of 11 to 13 spiral threads overriding less closely spaced axial ripples. Spiral threads sometimes—but not always—seen to extend backward a little distance beyond outer lip of protoconch. First two and a half to three and a half teleoconch whorls sculptured by three to four varices per whorl. Interspaces of varices with three to five axial ribs. Varices and axial ribs over-ridden by spiral threads. Varices gradually lost and replaced by axially elongated projections numbering nine or 10 per whorl. On last teleoconch whorls these projections are developed as pointed spines. Dorsal surface of

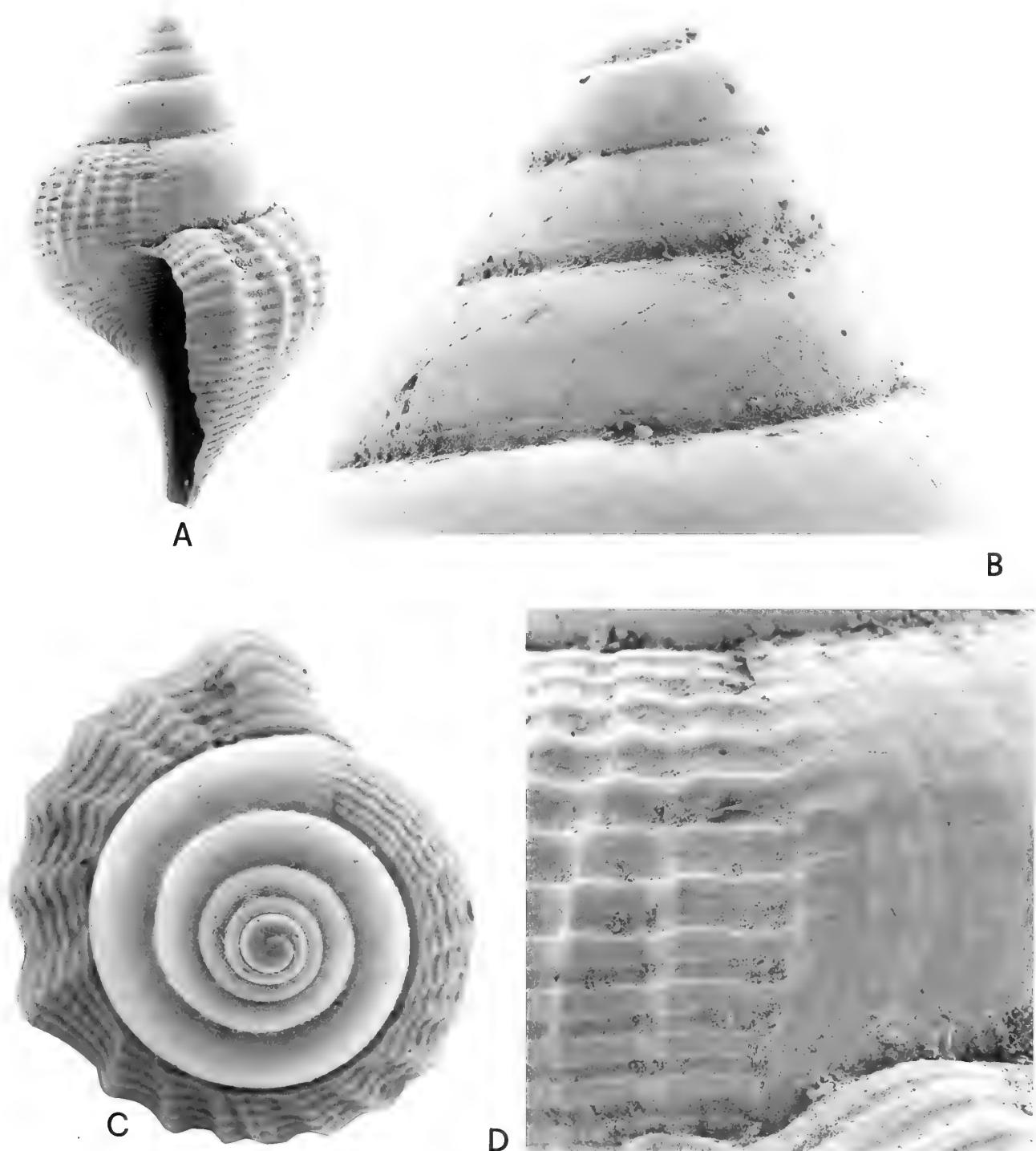


Figure 8. *Strombus (Lentigo) granulatus* Swainson. A-D. LACM 72-59.4. 75 feet, gravel and cobble, small islets off Quepos, Puntarenas Province, Costa Rica ($9^{\circ}22'12''N$, $84^{\circ}09'15''W$). A. From right side showing protoconch and first teleoconch whorl, $\times 35$. B. Enlargement of protoconch, $\times 200$. Note spiral sculpture near abapical suture. C. Apical view, $\times 55$. Note spiral ribs of teleoconch under outer lip of protoconch. D. Transition from protoconch to teleoconch, $\times 160$. Note opisthocyt growth lines of protoconch.

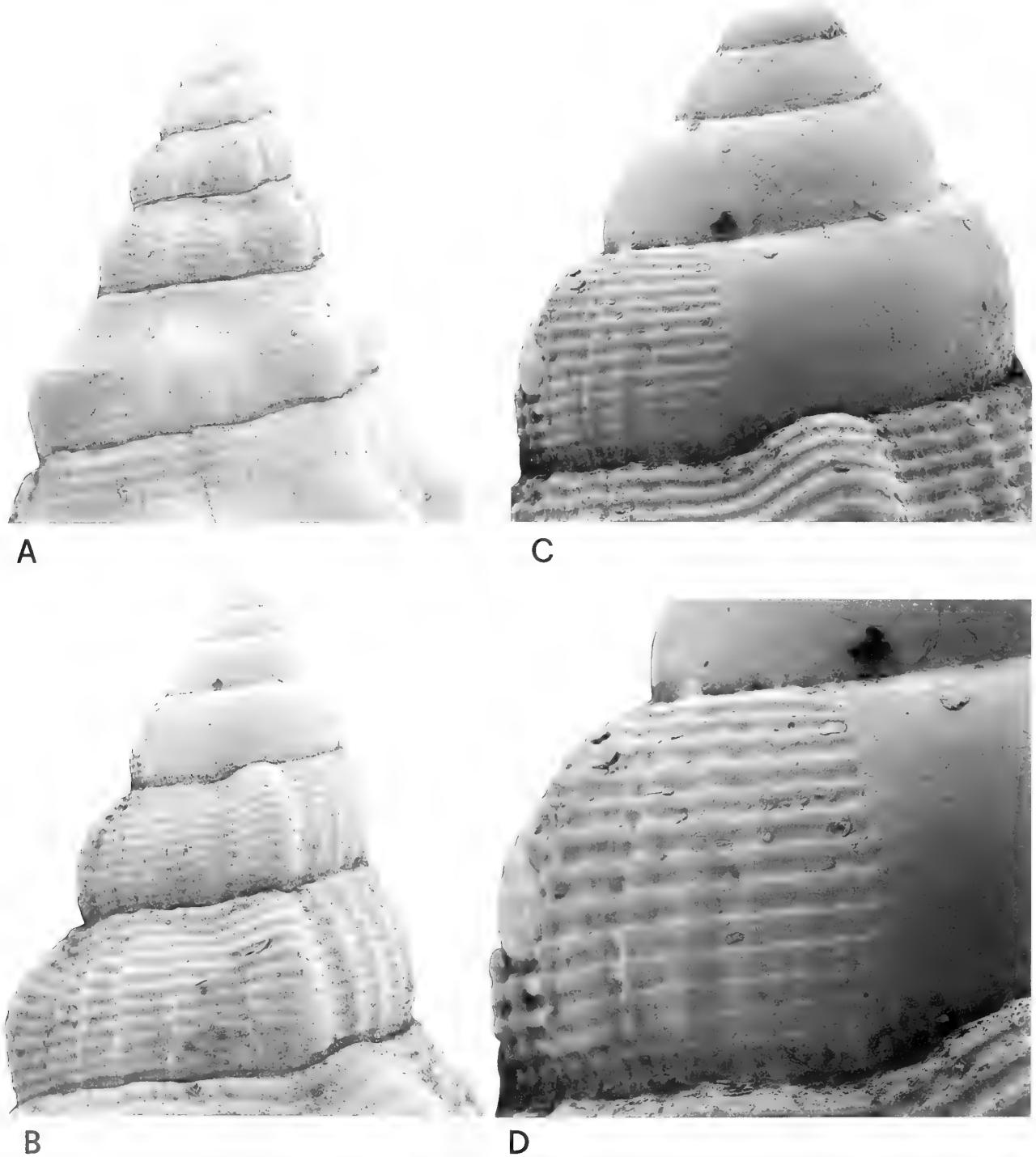


Figure 9. *Strombus (Lentigo) granulatus* Swainson. A-D. NMB H 17853. Dredged in 40 to 45 feet, Isla Pedro González, Archipiélago de las Perlas, Panama. A. Incomplete protoconch and early teleoconch whorls, $\times 12$. Note development of varices into subequal axial ribs and finally into axially elongated, slightly pointed knobs. B. Enlargement of same view as A, $\times 30$. C. Enlargement of incomplete protoconch, $\times 70$. D. Transition from protoconch to teleoconch, $\times 130$. In this specimen no spiral ribs of the teleoconch are visible under the outer lip of the protoconch.

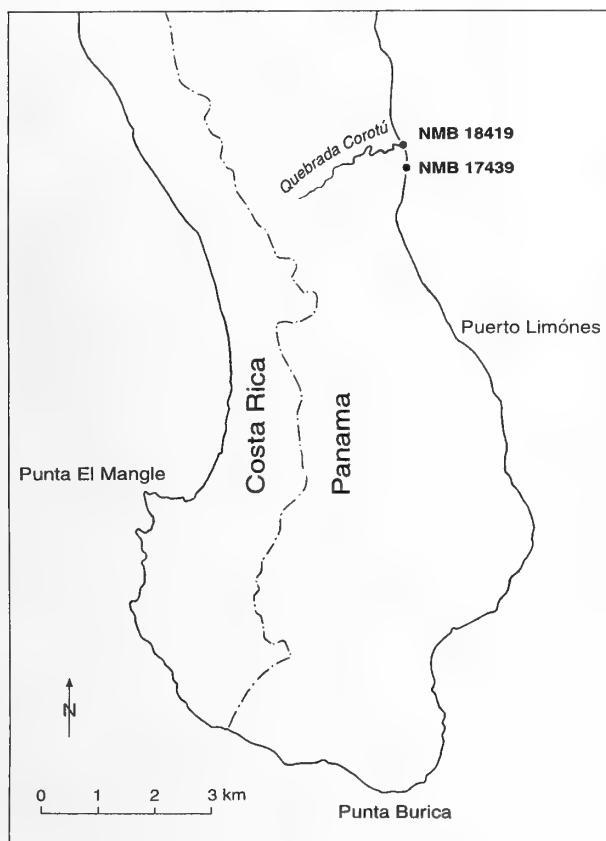


Figure 10. Map of the southern part of the Burica Peninsula, Chiriquí Province, Panama (for general location see number 2 of Figure 1). *S. granulatus* occurs at NMB localities 17439 and 18419, whereas *S. sp. D* has been found only at NMB locality 17439.

body whorl sculptured by three spiral rows of knobs sometimes over-ridden by spiral threads. Interspaces of rows of knobs sometimes—but not always—with three spiral threads. Aperture long and narrow. Parietal callus smooth. Outer lip somewhat flaring, its inner surface with a band of granulations. Lower part of outer lip with a moderately deep sinus. Base of columella bent backward.

Type: Not known. According to a letter from Kathie Way dated September 16, 1996, the type of this species is not in the collections of the Department of Zoology of The Natural History Museum, London; it was suggested that we inquire at the Department of Zoology of the National Museum of Wales in Cardiff, but Alison Trew of that institution gave a negative answer (letter dated September 26, 1996).

Remarks: We have studied a small number of Recent specimens of this species. We were especially interested in immature specimens in order to get photographs of complete protoconchs (Figure 8A–D) and to be able to

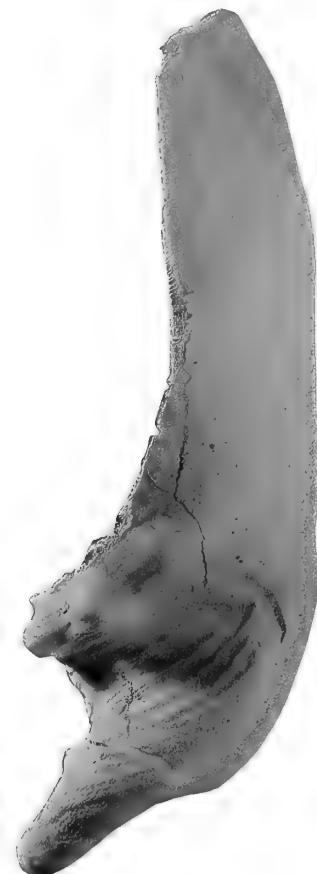


Figure 11. *Strombus (Lentigo) cf. granulatus* Swainson, NMB H 17847. NMB locality 18544 (= CJ-93-21-01 = PPP 01259); Ground Creek, northwestern part of Isla Colón, Bocas del Toro, Panama. Plio-Pleistocene. Height 80.8 mm. Fragment viewed from left side. $\times 1.5$.

recognize the development of the sculpture on early teleoconch whorls. As hinted at in the above description, it is interesting to observe that the earliest spiral sculpture is sometimes developed already under the outer lip of the protoconch. The surface of the protoconch is smooth with the exception of some opisthocyt growth lines near the outer lip and an ill-defined spiral sculptural element close to the abapical suture of the second and third volution.

The size of the adult shell and the intensity of the spiral sculpture are quite variable. Large specimens (height around 90 mm) have about eight teleoconch whorls, whereas small adult shells (height around 35 mm) have seven or seven and a half teleoconch whorls. These smaller adult shells are sometimes designated “dwarf variety” on museum labels. It would take a detailed statistical study based on a large amount of material to prove or disprove the existence of intermediates. For the time being *S. granulatus* is considered a variable species em-

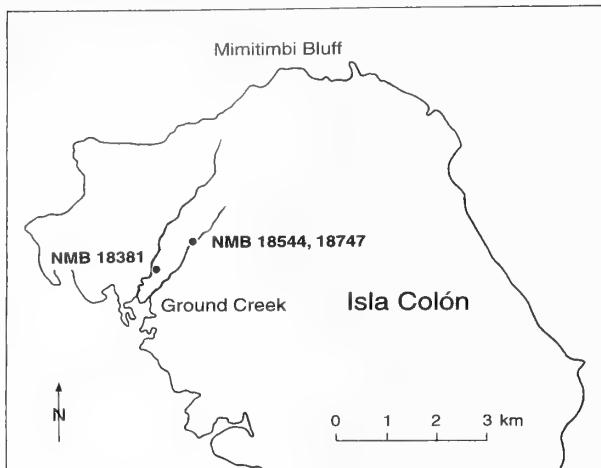


Figure 12. Map of the northern part of Isla Colón, Bocas del Toro, Panama, showing NMB localities 18381 and 18544, where *S. cf. granulatus* has been found, and NMB locality 18747, where *S. raninus* is recorded from (for general location see number 3 of Figure 1).

bracing large and small forms, a view also adopted by Emerson & Old (1963:9). Only four fossil specimens of this species are available: two from the Armuelles Formation (Pleistocene) of the southern Burica Peninsula, Panama, and two from the upper Onzole Formation (late Pliocene) of west of Camarones, Esmeraldas Province, Ecuador (Whittaker, 1988, fig. 2).

Comparisons: *Strombus granulatus* is the only species of the subgenus *Lentigo* in the Eastern Pacific. Occasional comparative remarks will be found under the fossil species discussed herein.

Material: For this paper we have used 16 lots with a total of 30 specimens as listed below:

1. 6 spec., LACM 33–121.4: shallow water, Bahía Honda, Veraguas, Panama ($7^{\circ} 43.77'N$, $81^{\circ} 31.90'W$).
2. 3 spec., LACM 39–62.6: 4–9 m, mud and sand, Isla Taboga, Panama ($8^{\circ} 48'N$, $79^{\circ} 30'W$).
3. 1 spec., LACM 66–28.5: low intertidal - 1.8 m, Bahía Partida, between Isla Partida and Isla Espíritu Santo, Gulf of California, Baja California Sur, Mexico ($24^{\circ} 31'N$, $110^{\circ} 23'W$).
4. 7 spec., LACM 72–59.4: 75 feet, gravel and cobble, small islets off Quepos, Puntarenas, Costa Rica ($9^{\circ} 22' 12''N$, $84^{\circ} 9' 15''W$).
5. 1 spec., Alvarez coll. 09873: Islas Secas, Golfo de Chiriquí, Panama. Dredged in 30 m.
6. 1 spec., Alvarez coll. 07564: Isla de los Pajaros, Archipiélago de las Perlas, Panama. Dredged in 45 feet.
7. 1 spec., Alvarez coll. 06572: Isla Saboga, Archipiélago de las Perlas, Panama. Dredged in 40–50 feet.
8. 1 spec., Alvarez coll. 06732: Isla Saboga, Archipiélago de las Perlas, Panama. Dredged in 28–35 feet.

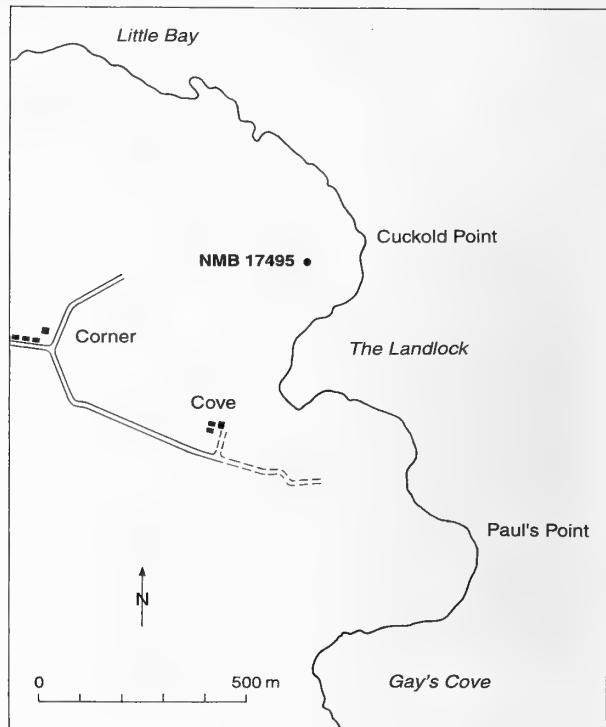


Figure 13. Map of part of northeastern Barbados, Lesser Antilles, showing NMB locality 17495, where *S. raninus* has been found (for general location see number 13 of Figure 1).

9. 1 spec., Alvarez coll. 09872: Islas Secas, Golfo de Chiriquí, Panama. Dredged in 30 m.
10. 1 spec., Alvarez coll. 09775: Isla Coiba, Golfo de Chiriquí, Panama. Dredged in 30–32 m.
11. 1 spec., Alvarez coll. 09675 (NMB H 17866): Isla Montuosa, Golfo de Chiriquí, Panama. Dredged in 25–30 m.
12. 1 spec., Alvarez coll. 02175 (NMB H 17867): Bahía San Telmo, Archipiélago de las Perlas, Panama. Dredged in 20–25 feet.
13. 1 spec., Alvarez coll. 2286 (NMB H 17853): Isla Pedro González, Archipiélago de las Perlas, Panama. Dredged in 40–45 feet.
14. 1 spec., NMB H 17843, NMB locality 17439 (= PJ 1757): 400 m S of Boca Quebrada Corotú, Burica Peninsula, Panama. Armuelles Formation (Pleistocene).
15. 1 spec., NMB H 17844, NMB locality 18419 (= CJ-87-04-37 = PPP 00144): 100 m S of Boca Quebrada Corotú, Burica Peninsula, Panama. Armuelles Formation (Pleistocene).
16. 2 spec., BMNH PI TG 4731-2: road-cutting about 1 km west of the village of Camarones, Esmeraldas Province, Ecuador. Upper Onzole Formation (late Pliocene).

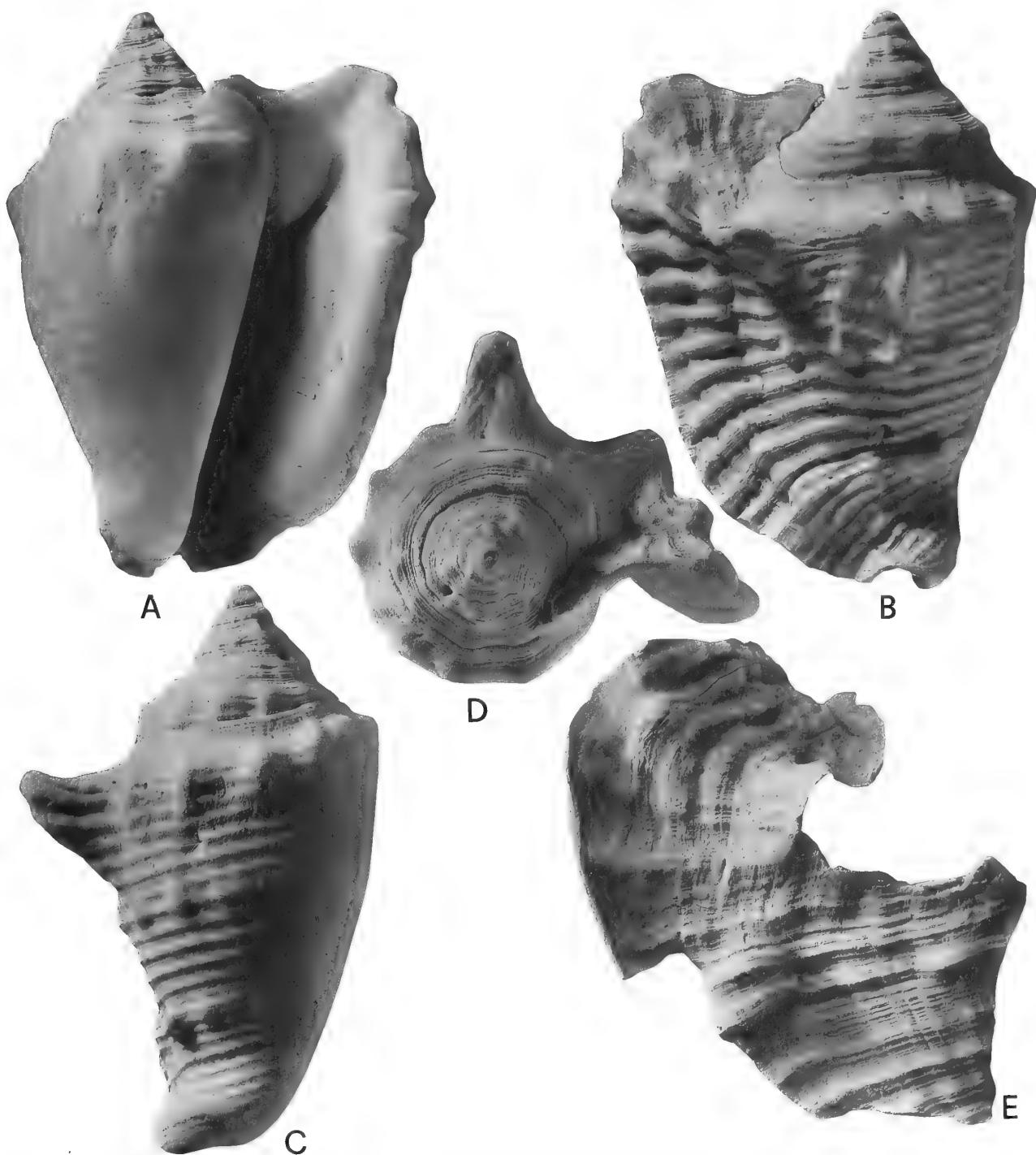


Figure 14. *Strombus (Lentigo) raninus* Gmelin. A–D. NMB H 17859. NMB locality 18750: Plantain Cays, outer coast of Valiente Peninsula, Bocas del Toro, Panama. Recent. Height 63.7 mm, width 46.9 mm. A. Front view. B. Rear view. C. From left side. D. Apical view. E. NMB H 17857. NMB locality 18747: Ground Creek, Isla Colón, Bocas del Toro, Panama. Pleistocene. Height 60.6 mm, width 48.5 mm. Rear view. Both specimens $\times 1.5$.

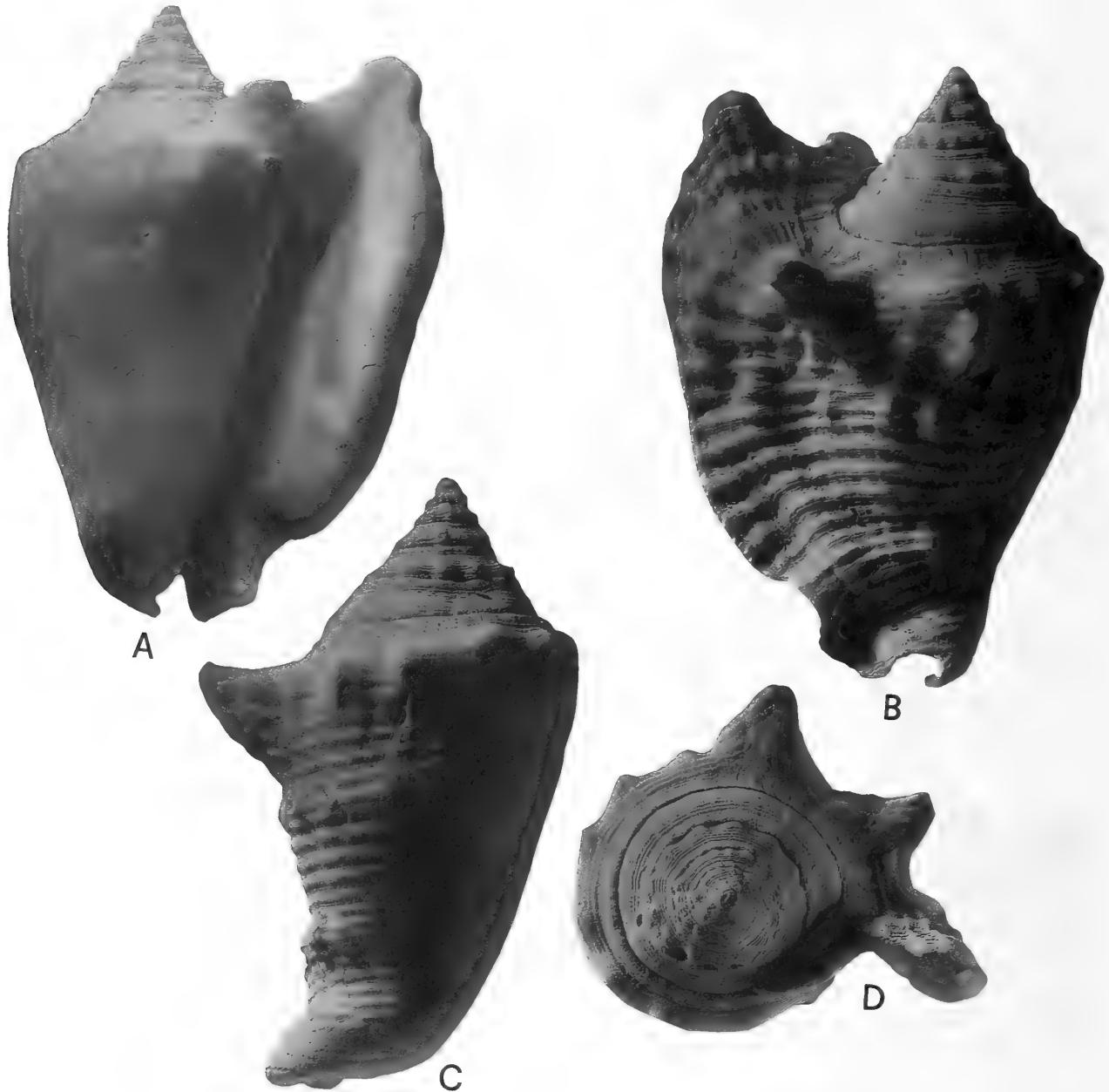
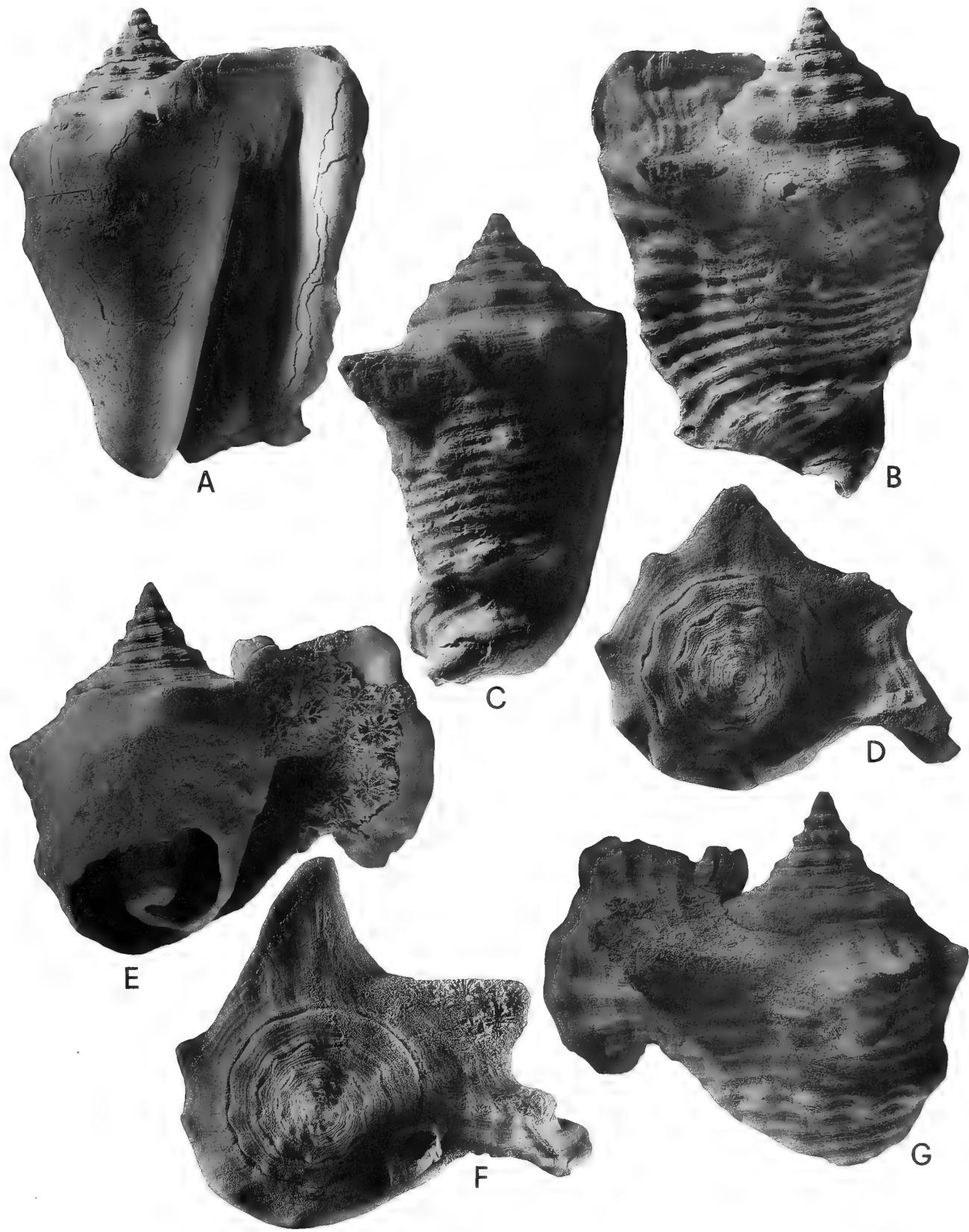


Figure 15. *Strombus (Lentigo) raninus* Gmelin. A–D. NMB H 17860. NMB locality 17692: Islas Chimanas, Estado Anzoategui, Venezuela. Recent. Height 64.1 mm, width 44.8 mm. A. Front view. B. Rear view. C. From left side. D. Apical view. $\times 1.5$.

→
Figure 16. *Strombus (Lentigo) raninus* Gmelin. A–D. NMB H 17861. NMB locality 17564: Laguna Boca Chica, Isla Margarita, Venezuela. Type locality of Boca Chica Formation (Holocene terrace). Height 58.9 mm, width 45.5 mm. A. Front view. B. Rear view. C. From left side. D. Apical view. E–G: NMB H 17856. NMB locality 18747: Ground Creek, Isla Colón, Bocas del Toro, Panama. Pleistocene. Height 45.8 mm, width 51.1 mm. E. Front view. F. Apical view. G. Rear view. Both specimens $\times 1.5$.



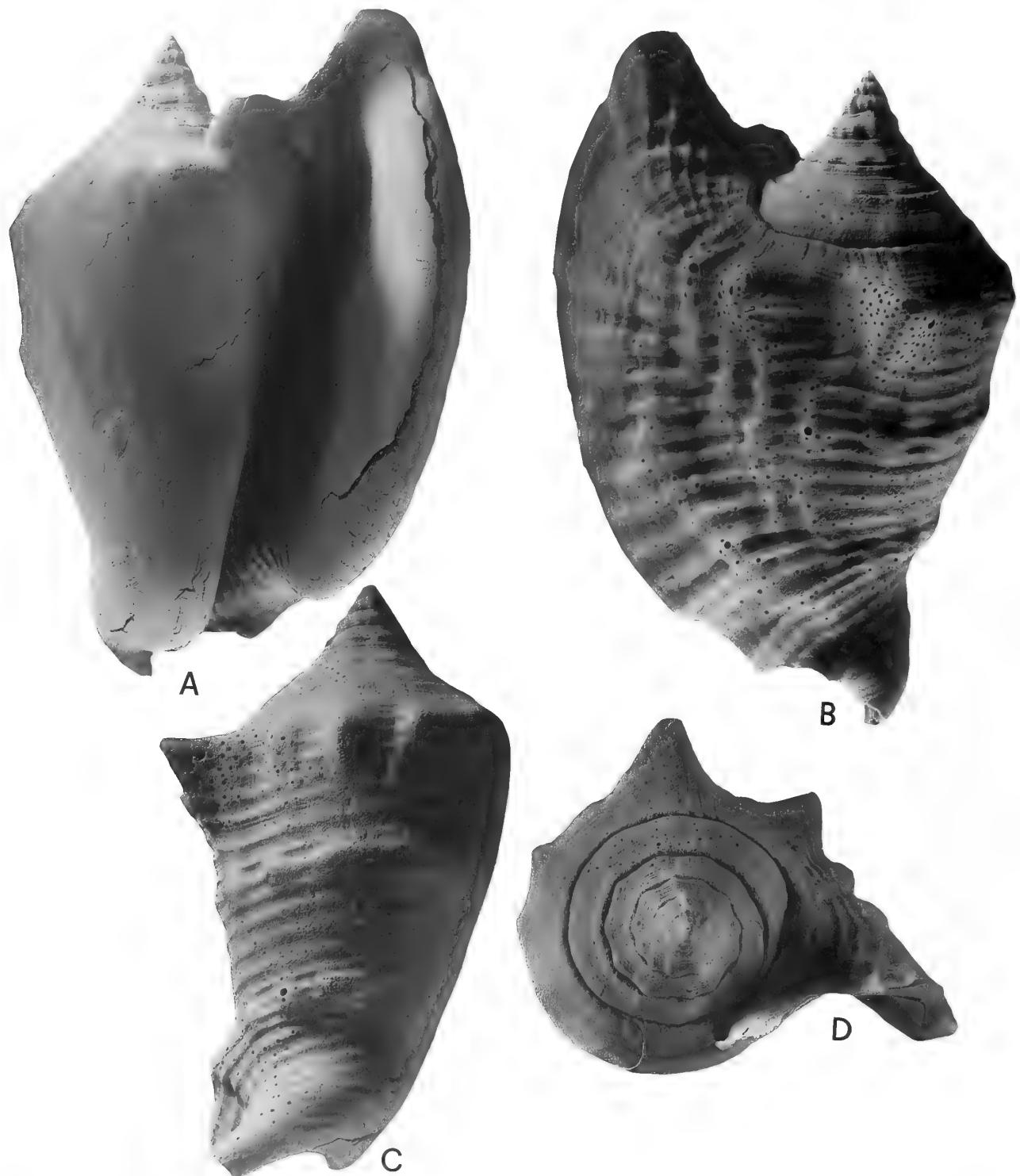


Figure 17. *Strombus (Lentigo) raninus* Gmelin. A–D. NMB H 17862. NMB locality 18940: Champ de Tir (rifle-range), Port-au-Prince, Haiti. Pleistocene. Height 80.0 mm, width 51.7 mm. A. Front view. B. Rear view. C. From left side. D. Apical view. $\times 1.5$.

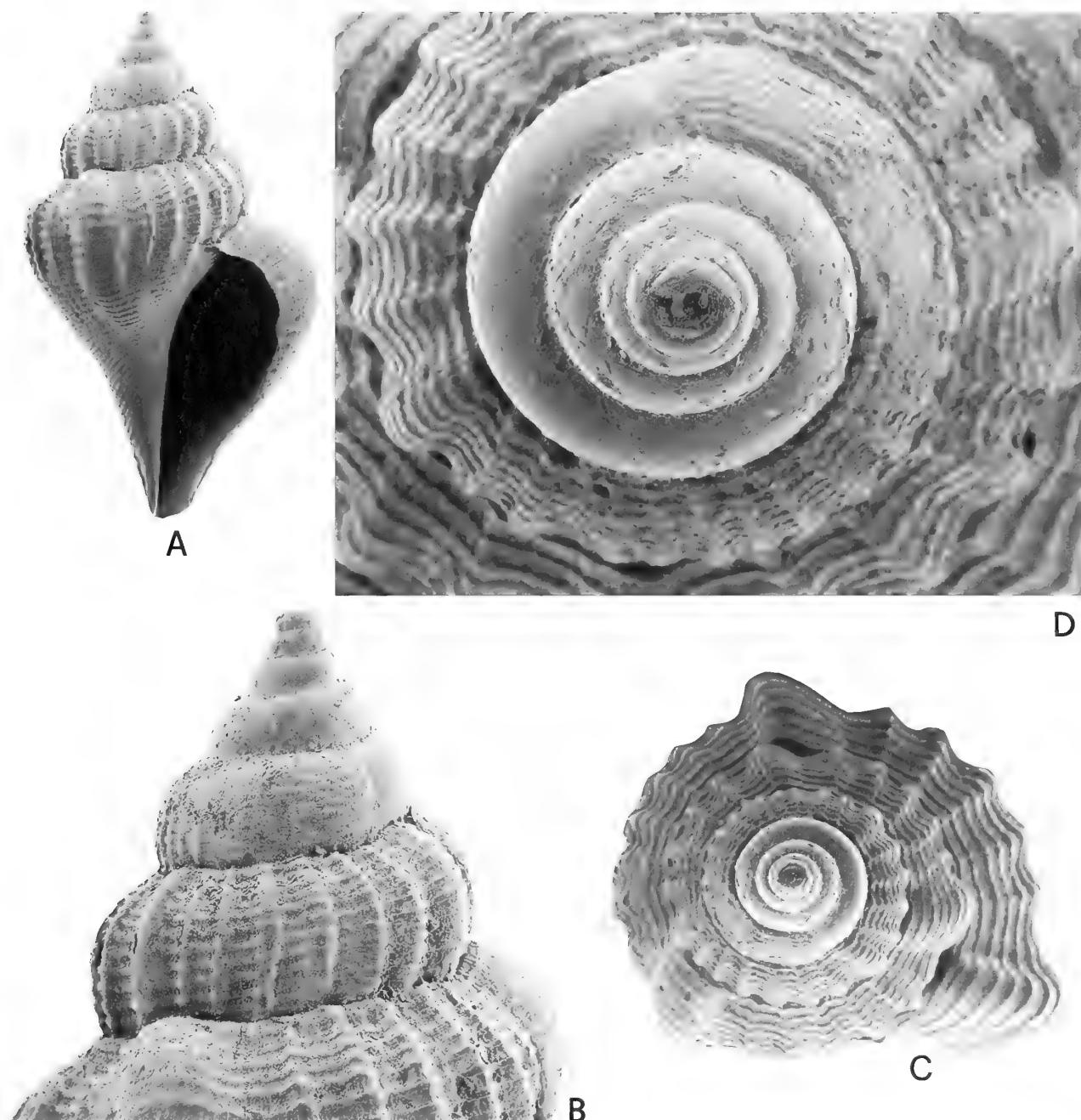


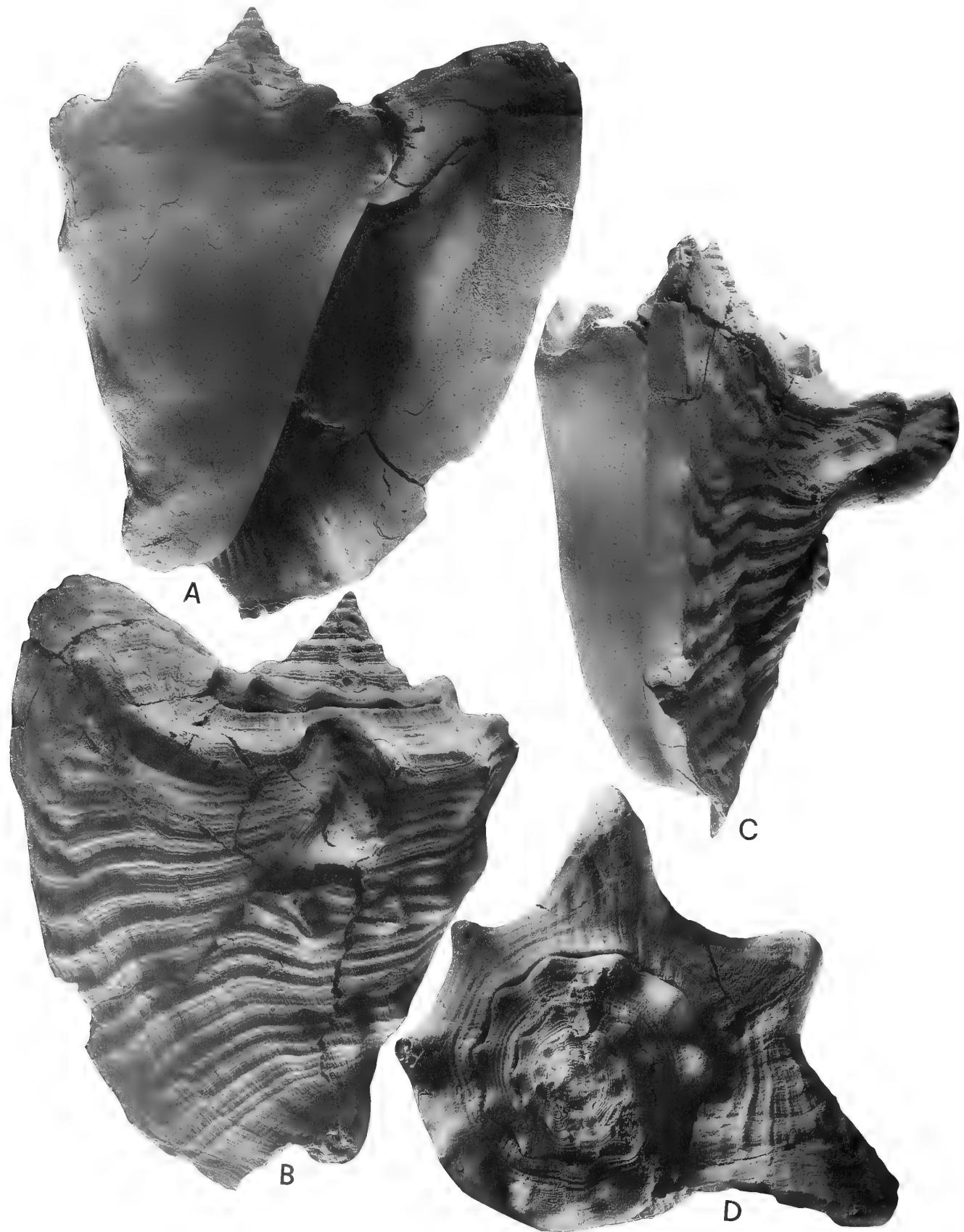
Figure 18. *Strombus (Lentigo) raninus* Gmelin. A–D. ANSP 285500. Near Isla Cancún, Territorio Quintana Roo, Yucatán, Mexico. Recent. A. Front view showing protoconch and the first three teleoconch whorls. $\times 12$. B. Enlargement of same view showing transition from protoconch to teleoconch and sculpture of early teleoconch whorls. $\times 30$. C. Apical view showing three varices per whorl. $\times 20$. D. Enlarged apical view. The initial volution of the protoconch is damaged. The protoconch seems to consist of four and a half to five volutions. $\times 60$.

Depth range and substratum: On exposed beaches of rock and sand; common in shallow water down to 75 m (Keen, 1971:421; Abbott, 1974:144).

Geographic distribution: The northern end of the Gulf

of California to Ecuador (Keen, 1971:421) and Galápagos Islands (Grant & Gale, 1931:755).

Occurrence: The Pliocene and Pleistocene occurrences of this species in Baja California, Mexico, have been list-



ed by Emerson & Old (1963:11). In Panama it is documented from two adjacent localities in the Armuelles Formation (Pleistocene) situated on the east coast of the Burica Peninsula (Figure 10). In Ecuador it is reported from the upper Onzole Formation (late Pliocene) of west of Camarones, Esmeraldas Province.

Strombus (Lentigo) cf. granulatus Swainson
(Figures 11, 12)

Remarks: Two fragmentary specimens are available. Both consist of the lower and strongly bent backward part of the columella, a portion of the parietal wall, and a small part of the dorsal surface of the body whorl.

The larger specimen has been photographed from the left side in order to show the lowest spiral row of knobs. The knobs are over-ridden by spiral threads. The specimen is of considerable size. Comparing it with a large Recent shell of *S. granulatus* it is estimated that it must have reached a height of about 120 mm.

The second specimen is smaller, but the preserved part of the dorsal surface of the body whorl is somewhat larger than that of the other specimen. It shows the beginning of a second spiral row of knobs.

Occurrence: NMB localities 18544 (= CJ-93-21-01 = PPP 01259) and 18381 (= PJ 2150 = CJ-93-56-01 = PPP 01286): both Ground Creek, northwestern part of Isla Colón, Bocas del Toro, Panama (Figure 12). Beds of Plio-Pleistocene age.

Strombus (Lentigo) raninus Gmelin
(Figures 12–18)

Strombus raninus Gmelin, 1791:3511; Bales, 1942:18, pl. 4, fig. c; Rice & Kornicker, 1962: 373, pl. 5, figs. 5, 10; Shoemaker, 1971:72; Humfrey, 1975:101, pl. 8, figs. 5, 5a–c; Odé, 1982:16.

Strombus tuberculatus Lamarck, 1822:690.

Strombus (Strombus) raninus Gmelin, Clench & Abbott, 1941:2, pl. 2.

Strombus (Tricornis) raninus Gmelin, Abbott, 1974:144, no. 1585, color plate 4.

Strombus raninus nanus Bales, 1942:19, pl. 4, figs. a–b.

Strombus wilsonorum Petuch, 1994:75, pl. 16, fig. K and p. 84, explanation of pl. 21, and p. 263.

Description: Shell solid, reaching a height of around 100 mm. Protoconch consists of about four and a half to five smooth volutions. Number of teleoconch whorls nine and a half. The first two to three teleoconch whorls usually

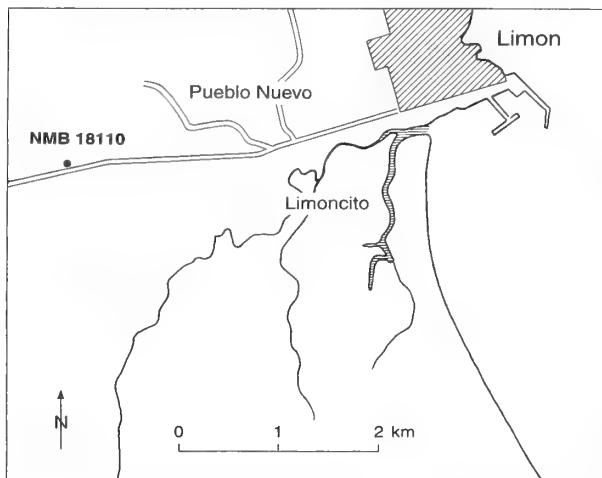


Figure 20. Map of the area of Limón, Costa Rica, showing NMB locality 18110, where *S. cf. raninus* has been found (for general location see number 1 of Figure 1).

with three primary axial ribs per whorl but sometimes without varices, i.e., with subequal axial ribs only. Space between primary axial ribs with three to seven secondary axial riblets. All the axial ribs and riblets are crossed by up to 10 spiral threads. On successive whorls the axial ribs gradually become subequal in size and are reduced to knobs situated on the shoulder of the whorl. The number of spiral threads on the spire whorl is somewhat reduced and their width is not equal. The two last knobs on the shoulder of the body whorl are spinelike and thus much larger than all the other knobs. Dorsal surface of body whorl sculptured by numerous fairly prominent spiral threads and two spiral rows of knobs. The abapical row ends near the edge of the outer lip at the position of the moderately deep stromboid notch. The adapical row of knobs is situated a little above the middle of the space between the abapical row and the shoulder of the body whorl. Outer lip thickened, its adapical end extended to below the position of the apex, in rare cases above it. Outer lip smooth except for some lirae at end below the stromboid notch and two to three ridges at the adapical end of the aperture. Parietal wall smooth. Base of columella strongly bent backward.

Type: Not known. Clench & Abbott (1941:3) selected a "type figure."

Type locality: Clench & Abbott (1941:3) designated

←
Figure 19. *Strombus (Lentigo) aff. raninus* Gmelin. A–D. NMB H 17806. NMB locality 18952 (= TU 1206): roadcut at K 17, highway from Santiago to San José de las Matas, west of bridge over Río Yaque del Norte at Santiago de los Caballeros, Dominican Republic. Gurabo Formation (probably early Pliocene part). Height 77.3 mm, width 67.4 mm. A. Front view. B. Rear view. C. From right side. D. Apical view. $\times 1.5$.

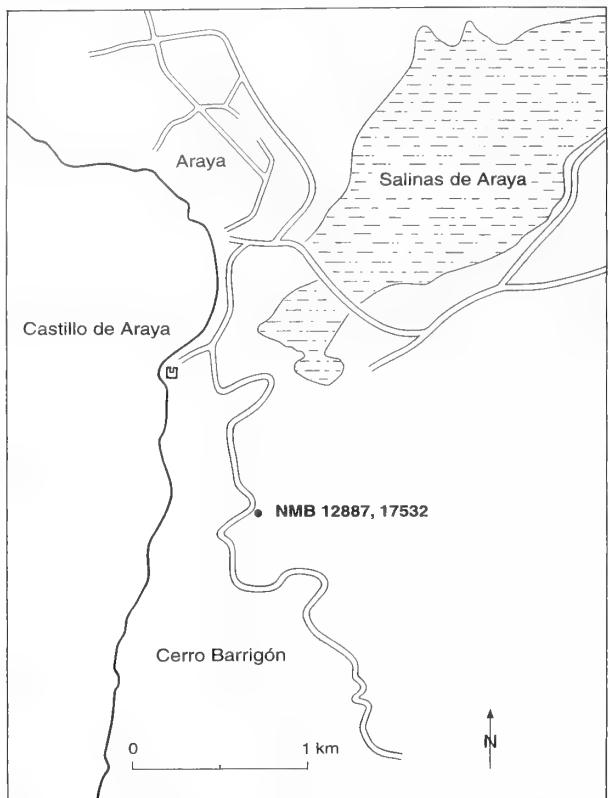


Figure 21. Map of area north of Cerro Barrigón, westernmost Araya Peninsula, Venezuela, showing NMB localities 12887 and 17532, where *S. barrigonensis* Jung & Heitz, sp. nov. has been found (for general location see number 9 of Figure 1).

Puerto Plata on the north coast of the Dominican Republic as the type locality.

Remarks: As indicated in the description, the axial sculpture of the early teleoconch whorls is strongly variable. There may be varices or not. When varices are present, their number is not constant. The limited amount of material studied for this paper does not allow us to be more precise except that we have seen rare specimens with four varices on early teleoconch whorls. The fact that there are specimens without varices at all might imply that the variability of the number of varices reaches from zero to four. However we have not seen specimens with one or two varices per early teleoconch whorl.

The above description is based on recent specimens from the Gibson-Smith collection and fossil specimens from six different locations (see under "Material"). Unfortunately, no well preserved protoconchs are available. Recent shells show some variability. Thus the extension of the adapical end of the outer lip is variable and there may be only one spinelike knob on the shoulder of the body whorl. *S. wilsonorum* Petuch (1994:75, pl. 16, fig. K and p. 84, explanation of pl. 21, and p. 263) from the Pleistocene of Florida clearly is a synonym of *S. raninus*.

The figured holotype closely resembles the specimen cited below from the Pleistocene of Haiti (Figure 16A–D).

Petuch (1994:75, pl. 16, fig. E and p. 84, explanation of pl. 21) assigned *S. raninus* to the subgenus *Lobatus* Iredale (1921:208). The name *Lobatus*, however, is an historical accident as explained by Abbott (1960:53) and is not available for a strombid subgenus.

As far as we are aware *S. raninus* has never been reported as a fossil (except for *S. wilsonorum* cited above). For this reason we are going to comment briefly on these fossil specimens from six different localities.

First: Two fragmentary specimens are available from the Pleistocene of Isla Colón, Bocas del Toro, Panama (NMB locality 18747: Figure 12). One has the adapical part of the outer lip and a portion of the dorsal side of the body whorl preserved (Figure 14E). The other consists of the spire and the adapical part of the body whorl (Figure 16E–G). The protoconch and the earliest teleoconch whorls of the latter are missing, and the first preserved teleoconch whorls are strongly eroded. One spiral row of knobs on the dorsal side of the body whorl can be recognized. A third specimen from the Pleistocene of Isla Colón (NMB locality 18381) is identified as *S. raninus* Gmelin? It is a well preserved fragment representing parts of the spire, but it is too incomplete for positive identification.

Second: There is single specimen from the Pleistocene of the neighborhood of Port-au-Prince, Haiti (NMB locality 18940) (Figure 17A–D). The protoconch and the first one or two teleoconch whorls are missing, but otherwise it is practically complete. Its surface is somewhat worn. The extension of the adapical end of the outer lip reaches above the apex, and the last knob on the shoulder of the body whorl is smaller than the second-last.

Third: An almost complete specimen (Figure 16A–D) has been collected from the Holocene of Isla Margarita, Venezuela (NMB locality 17564). The protoconch and the first teleoconch whorls are missing, and the edge of the outer lip, as well as the last knob on the shoulder of the body whorl, is somewhat damaged.

Fourth: A single specimen (NMB H 17873) with a broken apex and partly broken dorsal surface has been collected from a late Pleistocene terrace on the northeast coast of Barbados (NMB locality 17495: Figure 13). In an unpublished study by P. Büsser (University of Berne, 1980) an age of 82,000 years was assigned to this terrace. Two fairly well-preserved specimens from the Pleistocene of Bishopscourt, Barbados, are contained in the collections of the BMNH (G 10888).

Fifth: In the collections of the BMNH (GG 4921) there is an incompletely preserved specimen collected from a yellow marl of Holocene age of an unspecified locality on the island of Antigua.

Sixth: In February 1998, Dr. Jon Todd of the BMNH collected six fragments from the late Pliocene part of the Moín Formation of the Limón area, Costa Rica. One of

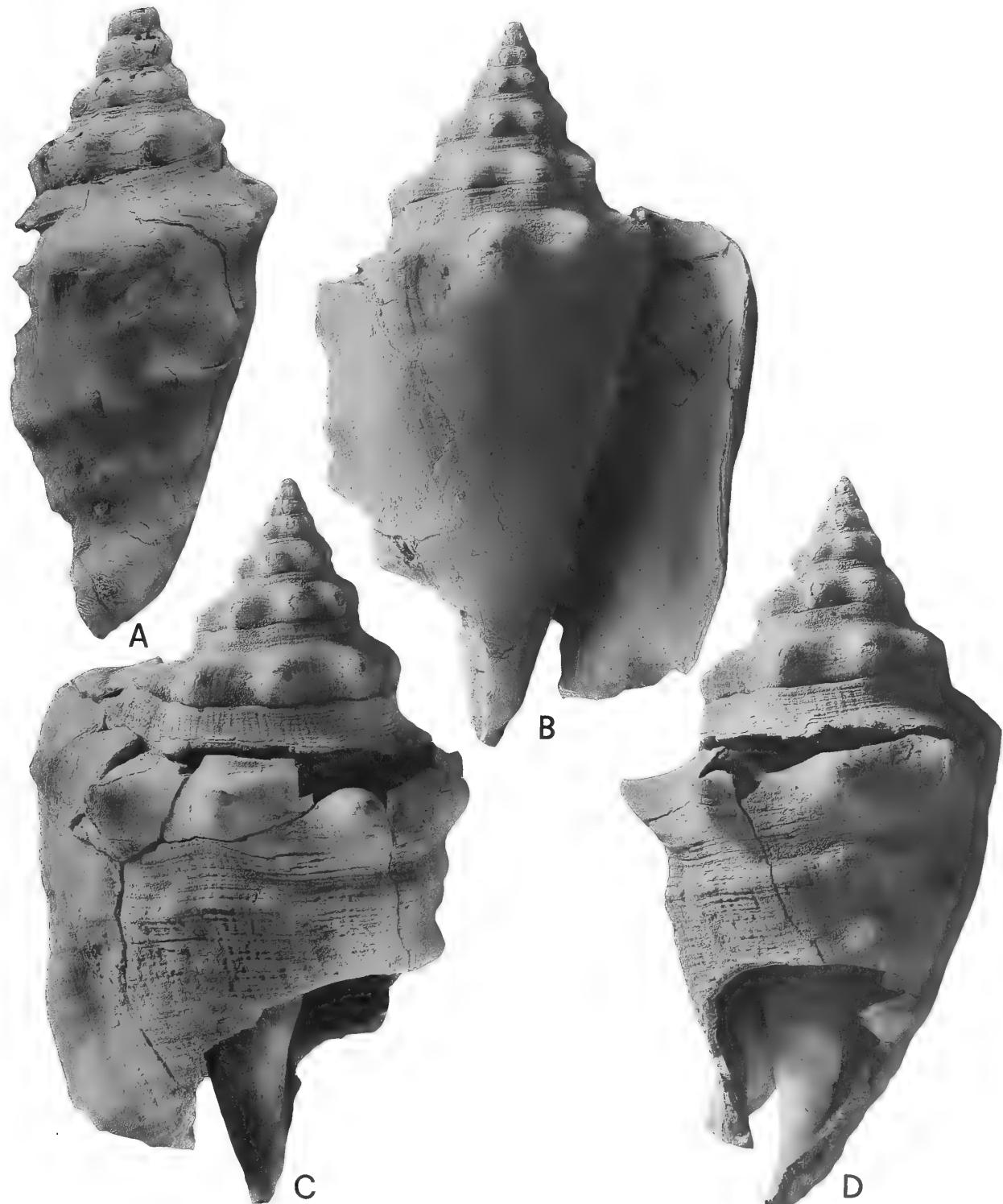


Figure 22. *Strombus (Lentigo) barrigonensis* Jung & Heitz, sp. nov. A–D. NMB locality 12887: north slope of Cerro Barrigón, Araya Peninsula, Venezuela. Cerro Negro Member of Cubagua Formation (early Pliocene). A. NMB H 17849. Paratype. Height 70.5 mm. Rear view. B–D NMB H 17848. Holotype. Height 81.6 mm, width 51.4 mm. B. Front view. C. Rear view. D. From left side. Both specimens $\times 1.5$.

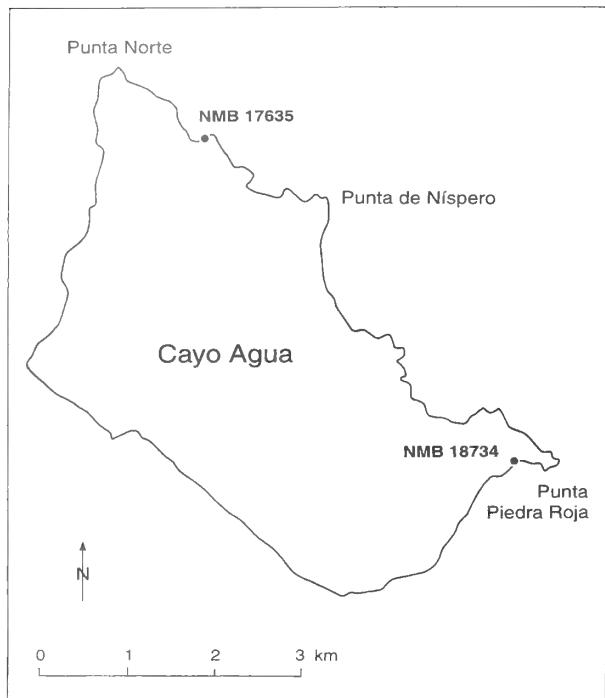


Figure 23. Map of Cayo Agua, Bocas del Toro, Panama, showing NMB locality 17635, where *S. toroensis* Jung & Heitz, sp. nov. has been found, and NMB locality 18734, from where *S. cf. fetus* Jung & Heitz, sp. nov. is recorded (for general location see number 4 of Figure 1).

the specimens is complete enough to be positive about the identification. Another fragment shows the spire with parts of the protoconch preserved.

Comparisons: *S. raninus* is morphologically dissimilar to any of the species discussed herein. *S. fetus* n. sp. has somewhat similar proportions but lacks the spinelike knobs on the shoulder of the body whorl.

Clench & Abbott (1941:3) considered *S. raninus* and *S. gallus* Linnaeus (1758:743) as closely related species. This statement was probably based on the long extension of the apical end of the outer lip. This extension may be extreme in *S. gallus* but never is in *S. raninus*. More importantly, *S. gallus* never has spiral rows of knobs on the dorsal side of the body whorl. We consider the latter feature as diagnostic for the subgenus *Lentigo*. *S. gallus* is therefore not included in *Lentigo*.

Material: For this paper we have used 20 lots with a total of 58 specimens as listed below:

1. 15 spec., NMB locality 17663: Punta La Salina (El Pico), west coast of the Paraguaná Peninsula, Falcón, Venezuela. Recent.
2. 11 spec., NMB locality 17675: between Naval Base of Puerto Cabello and Playa Quizandal, Borburata, Estado Carabobo, Venezuela. Recent.
3. 2 spec., NMB locality 17679: beach immediately

west of Playa Grande Yacht Club, Distrito Federal, Venezuela. Recent.

4. 2 spec., NMB locality 17685: about 1 km NE of Carenero, Laguna de Buche, Estado Miranda, Venezuela. Recent.
5. 3 spec., NMB locality 17686: Bahía Los Totumos, between Carenero and Cabo Codera, Estado Miranda, Venezuela. Recent.
6. 3 spec., NMB H 17860, NMB locality 17692: Islas Chimanas, Estado Anzoátegui, Venezuela. Recent.
7. 2 spec., NMB locality 17700: Islas Los Roques, Venezuela. Recent.
8. 1 spec., NMB locality 17702: Isla La Tortuga, Venezuela. Recent.
9. 1 spec., NMB H 17859, NMB locality 18750: Plantain Cays, outer coast of the Valiente Peninsula, Bocas del Toro, Panama. Recent.
10. 2 spec., ANSP 285500: near Isla Cancún, Territorio Quintana Roo, Yucatán, Mexico. Recent.
11. 3 spec., FMNH 177106: Lake Worth, Palm Beach County, Florida, USA. Recent.
12. 1 spec., USNM 269542: off Miami, Florida, USA. Recent.
13. 3 spec., USNM 890017: Peanut Island, Lake Worth, Florida, USA. Recent.
14. 1 spec., NMB H 17861, NMB locality 17564: Laguna de Boca Chica, Isla Margarita, Venezuela. Type locality of Boca Chica Formation (Holocene terrace). See Macsotay & Moore (1974:34, 41).
15. 1 spec., NMB H 17862, NMB locality 18940: Champ de Tir (= rifle-range), Port-au-Prince, Haiti. Pleistocene.
16. 2 spec., NMB H 17856 and H 17857, NMB locality 18747 (= PJ 2284 = PPP 02250): Ground Creek, Isla Colón, Bocas del Toro, Panama. Pleistocene.
17. 1 spec., NMB H 17873, NMB locality 17495: Barbados, northeast coast; near "The Landlock." Coordinates: 662.250E/1471.780N. Terrace of young Pleistocene age.
18. 2 spec., BMNH G 10888: Bishopscourt, Barbados. Low level reefs, Pleistocene.
19. 1 spec., BMNH GG 4921: unspecified locality on Antigua, Lesser Antilles. From a yellow marl of Holocene age.
20. 6 spec., BMNH PI TG 4733/38: Route 32, 3 km west of Puerto Limón, Costa Rica. Basal Moín Formation, late Pliocene (1.5–1.9 my).

Depth range: 1 foot (0.3 m) (Humfrey, 1975:102) to 30 fathoms (about 55 m) (Odé, 1982:16).

Substratum: On offshore coral reefs and somewhat deeper algal environment (Odé, 1982:16); on eel grass beds (Humfrey, 1975:102); on grassy bottoms (Rios, 1985:62).

Geographic distribution: North Carolina to Florida,

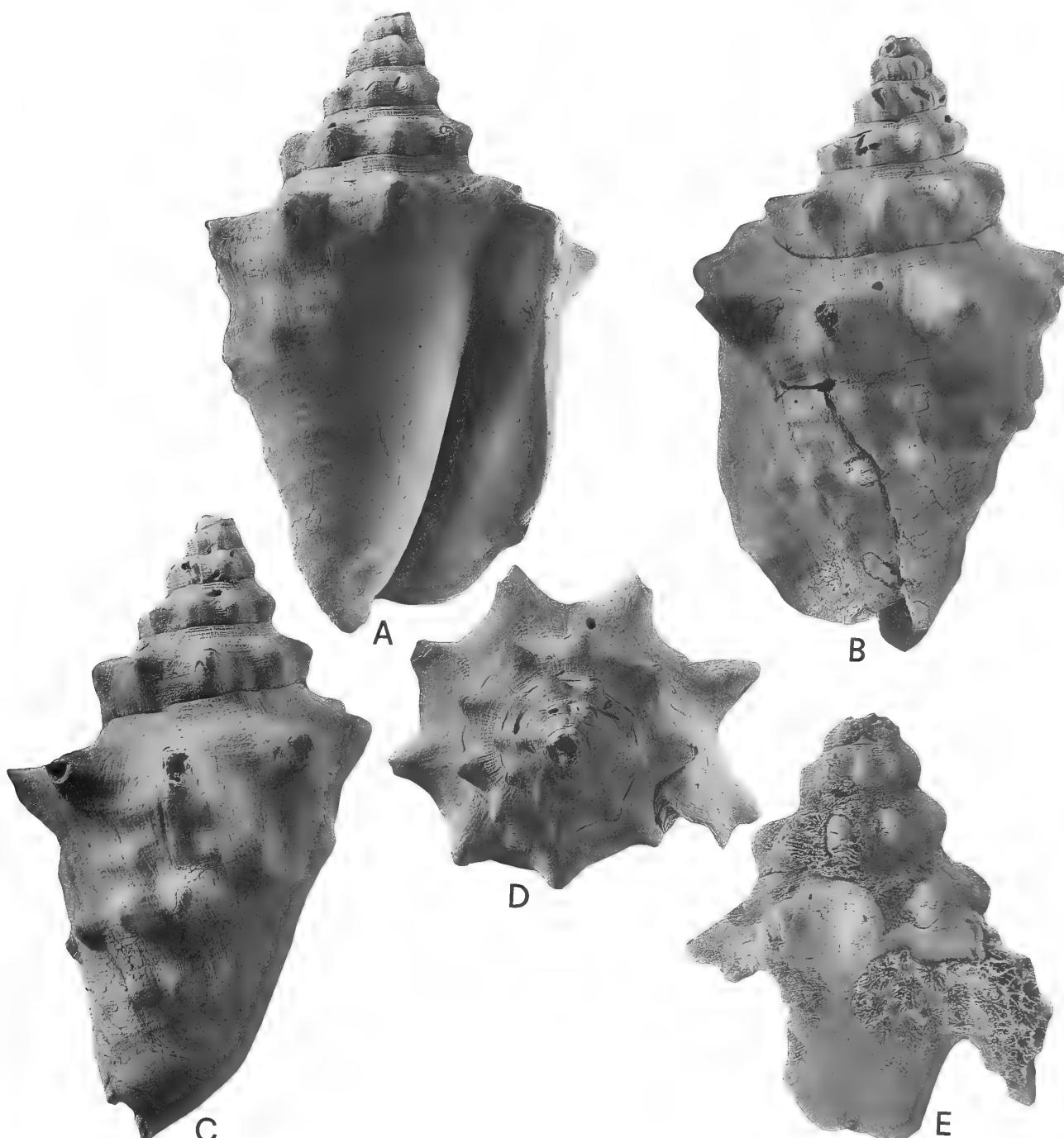


Figure 24. *Strombus (Lentigo) toroensis* Jung & Heitz, sp. nov. A–E. NMB locality 17635: northeast coast of Cayo Agua, Bocas del Toro, Panama; about 1.3 km southeast of Punta Norte. Cayo Agua Formation (early Pliocene). A–D, NMB H 17865. Holotype. Height 69.3 mm, width 42.3 mm. A. Front view. B. Rear view. C. From left side. D. Apical view. E. NMB H 17845. Paratype. Height 47.2 mm, width 41.7 mm. Front view. Both specimens $\times 1.5$.

Bermuda (Odé, 1982:16), Gulf of Mexico (Springer & Bullis, 1956:26; Lipka, 1974:150), West Indies, northern Colombia, Venezuela, Surinam, Brasil (Amapá to Rio Grande do Norte) (Rios, 1985:62).

Occurrence: The fossil occurrences include the late Pliocene of the Limón area, Costa Rica; the Pleistocene of Isla Colón, Bocas del Toro, Panama; the Pleistocene near Port-au-Prince, Haiti; the late Pleistocene of Barbados;

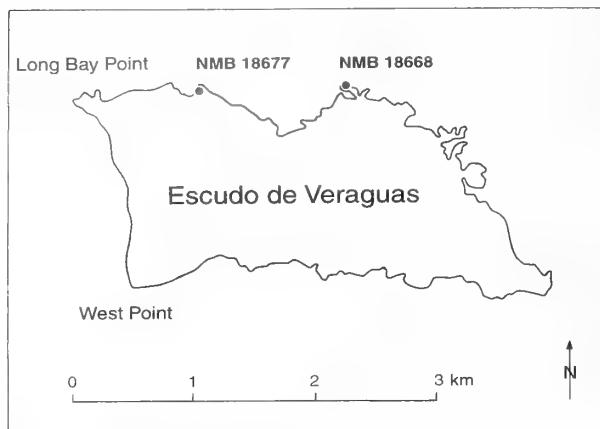


Figure 25. Map of the island of Escudo de Veraguas, Bocas del Toro, Panama, showing NMB locality 18677, where *S. fetus* Jung & Heitz, sp. nov. has been found, and NMB locality 18668, from where *S. insulanus* Jung & Heitz, sp. nov. is recorded (for general location see number 6 of Figure 1).

the Holocene (MacSotay & Moore, 1974:34, 41) of Isla Margarita, Venezuela, and the Holocene of Antigua.

Strombus (Lentigo) aff. raninus Gmelin

(Figure 19)

Remarks: A single fairly complete and fairly well-preserved specimen is available. It is the only specimen of *Lentigo* known from the Dominican Republic; it had been collected by Harold and Emily Vokes from a locality (TU 1206) near Santiago. Vokes (1989:46) assigned this locality to the Gurabo Formation.

The protoconch of the specimen is incomplete. The lirae on the abapical part of the outer lip and the sharp, elevated lirae near the adapical canal of the aperture are practically the same as those of *S. raninus*. However, the early teleoconch whorls carry only three primary axial ribs and not four as in *S. raninus*. But the main difference between the two species concerns the general shape of the spire. In *S. raninus* the spire is rather high, whereas in *S. aff. raninus* it is sunken. In other words, the slope of the last three teleoconch whorls in *S. raninus* is steep, but in *S. aff. raninus* rather flat.

Occurrence: NMB locality 18952 (= TU 1206): roadcut at K 17, highway from Santiago to San José de las Matas, west of bridge over Río Yaque del Norte at Santiago de los Caballeros, Dominican Republic (see Saunders et al., 1986:64), Gurabo Formation (probably early Pliocene part).

Strombus (Lentigo) cf. raninus Gmelin

(Figure 20)

Remarks: Two fragmentary specimens are available. Both are too incomplete to be figured. The larger frag-

ment (height 38.2 mm) (NMB H 17874) consists of the columella, part of the spire, and a small part of the dorsal surface of the body whorl carrying the beginning of a spiral row of knobs. The smaller fragment (height 15.4 mm, width 9.9 mm) (NMB H 17875) consists of a few spire whorls.

Occurrence: NMB locality 18110 (= PJ 2033 = CJ-89-38-2 = PPP 00718); about 2 km west of Cementerio of Limón, Costa Rica; north side of main road (Figure 20). Moín Formation (late Pliocene).

Strombus (Lentigo) barrigoniensis Jung & Heitz,
sp. nov.

(Figures 21, 22)

Etymology: Named after Cerro Barrigón, near the western end of the Araya Peninsula, Venezuela.

Description: Shell reaching a height of about 80 mm, moderately slender. Protoconch and earliest teleoconch whorls not known. Earliest preserved teleoconch whorls sculptured by eight axial ribs per whorl, which are overridden by eight spiral threads. On later teleoconch whorls the axial ribs gradually develop into knobs and on the dorsal side of the body whorl into spines. Number of knobs or spines on last whorl 10. Number of spiral threads on penultimate whorl 13. Number of preserved teleoconch whorls seven. Dorsal surface of body whorl with three spiral rows of knobs. The most adapically situated row not prominent, the others prominent. Remainder of dorsal side of body whorl sculptured by spiral and axial threads. Aperture long and narrow. Parietal callus smooth. Outer lip only slightly flaring, its inner surface smooth with the exception of a few faint, spirally elongated denticles on the adapical and abapical part. Sinus small. Base of columella bent backward.

Holotype: NMB H 17848 (Figure 21B–D).

Dimensions of holotype: Height 81.6 mm; width 51.4 mm.

Type locality: NMB locality 12887 (= PJ 1015). North slope of Cerro Barrigón, Araya Peninsula, Venezuela (Figure 21). Cerro Negro Member of Cubagua Formation (early Pliocene).

Remarks: This species is based on eight incomplete, partly fragmentary specimens. The holotype is the most complete shell.

Comparisons: *S. barrigoniensis* cannot be compared directly with any of the species described herein. There is a superficial resemblance to *S. fetus* n. sp., but that species has a larger apical angle, a much more prominent spiral sculpture on the body whorl, and more knobs per whorl. The form recorded below under the name of *Strombus (Lentigo) species A* is much more slender and



Figure 26. A–D. *Strombus (Lentigo) fetus* Jung & Heitz, sp. nov. NMB H 17854. Holotype. NMB locality 18677: north coast of Escudo de Veraguas, Bocas del Toro, Panama; 1 km east of Long Bay Point. Escudo de Veraguas Formation (late Pliocene). Height 64.4 mm, width 48.8 mm. A. Front view. B. Rear view. C. From right side. D. From left side. E. *Strombus (Lentigo) cf. fetus* Jung & Heitz, sp. nov. NMB H 17855. NMB locality 18734: 300 m westnorthwest of Punta Piedra Roja, Cayo Agua, Bocas del Toro, Panama. Cayo Agua Formation (middle Pliocene). Height 46.1 mm, width 28.2 mm. Rear view. Both specimens $\times 1.5$.

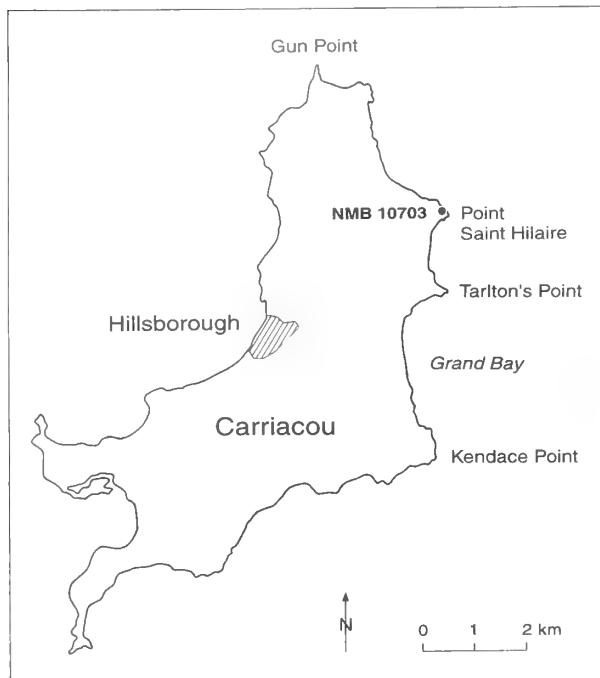


Figure 27. Map of the island of Carriacou, Grenadines, Lesser Antilles, showing NMB locality 10703, where *S. cf. insulanus* Jung & Heitz, sp. nov. has been found (for general location see number 12 of Figure 1).

lacks the fairly prominent axial threads on the body whorl. For comparative remarks concerning *S. toroensis* see under that species.

Material: There are only two lots with a total of eight specimens as listed below:

1. 4 spec., NMB locality 12887 (= PJ 1015): north slope of Cerro Barrigón, Araya Peninsula, Venezuela. Cerro Negro Member of Cubagua Formation (early Pliocene). Holotype and 3 paratypes.
2. 4 spec., NMB locality 17532 (= GS-8-ARY): same locality as NMB locality 12887 (see above). Paratypes.

Measurements: Due to the incomplete preservation of the available specimens, no meaningful measurements can be made.

Occurrence: Known only from the type locality: North slope of Cerro Barrigón, Araya Peninsula, Venezuela. Cerro Negro Member of Cubagua Formation (early Pliocene).

Strombus (Lentigo) toroensis Jung & Heitz, sp. nov.
(Figures 23, 24)

Etymology: Referring to the Province of Bocas del Toro.

Description: Shell reaching a height of about 70 mm,

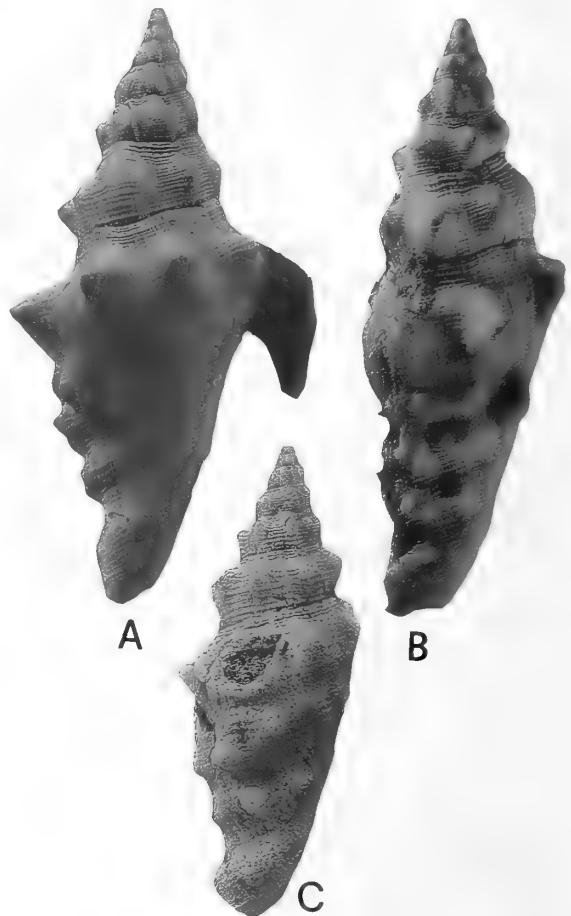


Figure 28. A, B. *Strombus (Lentigo) insulanus* Jung & Heitz, sp. nov. NMB H 17842. Holotype. NMB locality 18668: near the middle of the north coast of Escudo de Veraguas, Bocas del Toro, Panama. Escudo de Veraguas Formation (middle Pliocene). Height 53.2 mm, width 29.0 mm. A. Front view. B. From left side. C. *Strombus (Lentigo) cf. insulanus* Jung & Heitz, sp. nov. NMB H 17846. NMB locality 10703: 150 m northwest of Point Saint Hilaire, Carriacou, Grenadines, Lesser Antilles. Grand Bay Formation (early middle Miocene). Height 41.9 mm, width 16.6 mm. Rear view. Both specimens $\times 1.5$.

moderately slender. Protoconch and earliest teleoconch whorls not known. Earliest preserved teleoconch whorls sculptured by three primary axial ribs per whorl with first five, then four, and later three and two secondary axial riblets in their interspaces. Primary and secondary axial ribs are all over-ridden by 10 spiral riblets. Secondary spiral riblets are introduced at an early stage. On later teleoconch whorls there are 10 subequal knobs per whorl, which become somewhat pointed on the body whorl. Number of knobs on body whorl nine. Dorsal surface of body whorl with three spiral rows of knobs. The most adically situated row not prominent, the central row prominent, and the third, most abically situated row less prominent than the central row. Remainder of dorsal



Figure 29. *Strombus (Lentigo)* sp. A. A, B. NMB locality 17530: 30 m west of Carrizal Cemetery, a little less than 3 km northeast of La Vela, Falcón, Venezuela. Mataruca Member of Caujara Formation (late Miocene). A. NMB H 17850. Rear view. Height 59.0 mm, width 36.8 mm. B. NMB H 17851. From left side. Height 62.7 mm. Both specimens $\times 1.5$.

surface of body whorl sculptured by numerous faint axial and spiral threads. Aperture long and narrow. Parietal callus smooth. Outer lip a little flaring, its inner surface smooth except for a few spirally elongated denticles near the shallow sinus. Base of columella bent backward.

Holotype: NMB H 17865 (Figure 23A–D)

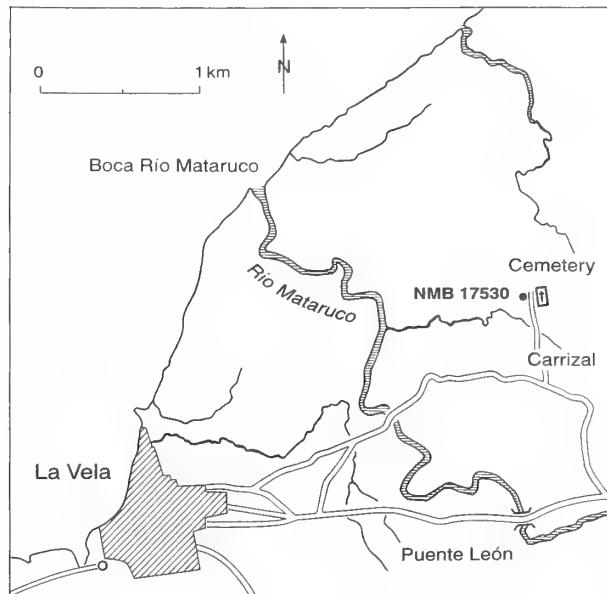


Figure 30. Map of the area northeast of La Vela, Falcón, Venezuela, showing NMB locality 17530, where *S. sp. A* is recorded from (for general location see number 9 of Figure 1).

Dimensions of holotype: Height 69.3 mm; width 42.3 mm.

Type locality: NMB locality 17635 (= PJ 1817 = CJ-87-32-01 = PPP 00201): northeast coast of Cayo Agua, Bocas del Toro, Panama; about 1.3 km southeast of Punta Norte (Figure 23). Cayo Agua Formation (early Pliocene).

Remarks: This species is based on two specimens from the same locality. The smaller specimen, the figured paratype (Figure 24E) is an incompletely preserved shell consisting of three late whorls and the adapical part of the aperture. The holotype is more complete and consists of five and a half teleoconch whorls.

Comparisons: *S. toroensis* is somewhat similar to *S. barrigonensis*, but at the same time clearly distinct from it. *S. barrigonensis* is sculptured by eight subequal axial ribs on early teleoconch whorls, whereas *S. toroensis* has three primary axial ribs per whorl with secondary axial riblets in the interspaces. Both species have a similar apical angle. The base of the columella is more strongly bent backward in *S. toroensis*.

Material: As mentioned above, only two specimens from the same locality are available.

Measurements: Due to the incomplete preservation no meaningful measurement can be made.

Occurrence: Known only from the type locality: about 1.3 km southeast of Punta Norte, Cayo Agua, Bocas del

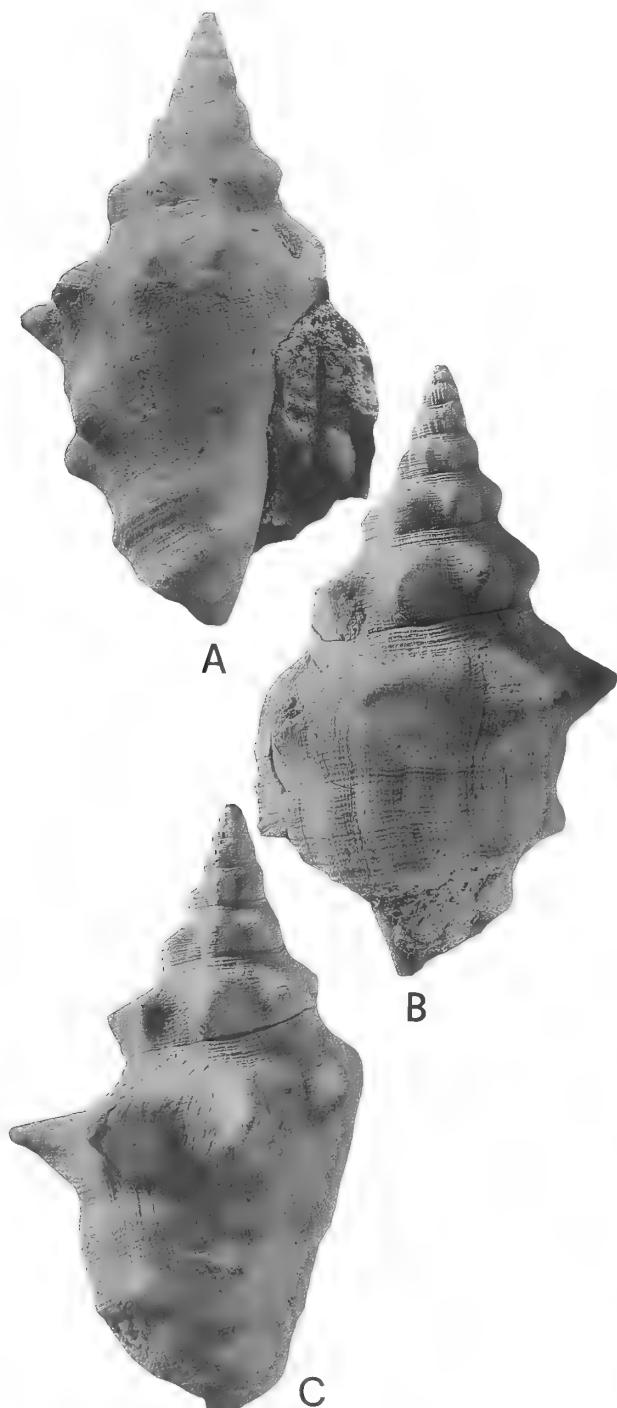


Figure 31. *Strombus (Lentigo)* sp. B. A–C. NMB H 17852. NMB locality 18716: southwest coast of Valiente Peninsula, Bocas del Toro, Panama; 5 km southeast of Cayo Patterson, at south end of Playa Lorenzo. Nancy Point Formation (late Miocene). Height 54.9 mm, width 34.1 mm. A. Front view. B. Rear view. C. From left side. $\times 1.5$.

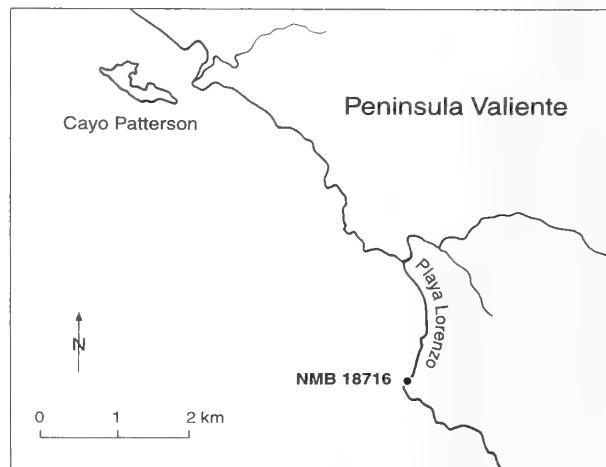


Figure 32. Map of part of the southwestern coast of the Valiente Peninsula, Bocas del Toro, Panama, showing NMB locality 18716, where *S. sp. B* has been found (for general location see number 5 of Figure 1).

Toro, Panama (Figure 23). Cayo Agua Formation (early Pliocene).

Strombus (Lentigo) fetus Jung & Heitz, sp. nov.

(Figures 25, 26A–D)

Etymology: Latin fetus = full, filled, pregnant.

Description: Shell reaching a height of about 65 mm, rather stout. Protoconch not known. Earliest teleoconch whorls corroded. Number of preserved teleoconch whorls

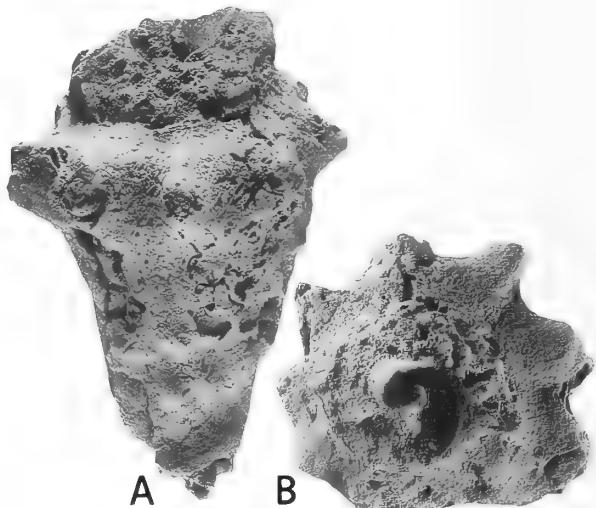


Figure 33. *Strombus (Lentigo)* sp. C. A, B. NMB H 17858. NMB locality 17526: 200 m south of El Porvenir and 7 km westnorthwest of Pueblo Nuevo, Paraguaná Peninsula, Falcón, Venezuela. El Porvenir beds (middle or late Miocene). Height 44.2 mm, width 31.3 mm. A. Rear view. B. Apical view. $\times 1.5$.



Figure 34. Map of part of the central Paraguaná Peninsula, Falcón, Venezuela, showing NMB locality 17526, where *S. sp. C* has been found (for general location see number 8 of Figure 1).

eight. Sculpture of early teleoconch whorls consists of 20 or a little more axial ribs, which are crossed by nine spiral threads. A shoulder situated a little below the middle of the height of the whorl is gradually developed. Simultaneously that part of the axial ribs situated above the developing shoulder gradually disappears. The axial ribs then are transformed into moderately prominent knobs. Profile of whorls above the shoulder straight on earlier whorls, somewhat concave on later whorls. Number of knobs on late whorls 12 to 13. Dorsal surface of body whorl sculptured by 10 primary spiral ribs below the shoulder and one to two secondary spiral threads on some of the interspaces. There are two spiral ridges with more prominent knobs below the shoulder. Growth lines near the outer lip prominent. Sculpture on and above the

shoulder consists of nine spiral riblets near the outer lip. Aperture long and narrow. Outer lip flaring. Parietal callus smooth except for a few spirally directed wrinkles near the adapical end of the aperture. Inner surface of outer lip smooth with the exception of a few spirally ori-

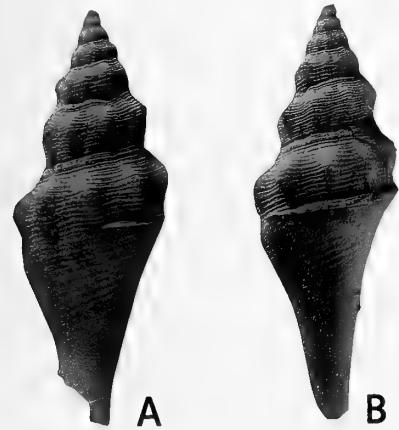


Figure 35. *Strombus (Lentigo)* sp. D. A, B. NMB H 17863. NMB locality 17439: 400 m south of Boca Quebrada Corotú, east coast of Burica Peninsula, Chiriquí, Panama. Armuelles Formation (Pleistocene). Height 36.9 mm, width 14.3 mm. A. Rear view. B. From left side. $\times 1.5$.

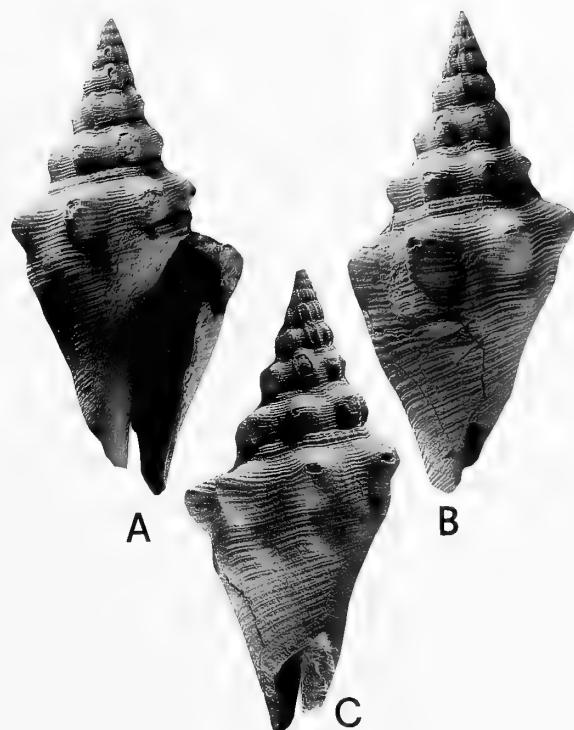


Figure 36. *Strombus (Lentigo)* sp. E. A-C. NMB H 17864. NMB locality 10635: Bowden, Port Morant, Jamaica. Bowder Formation (early Pliocene). Height 42.3 mm, width 20.6 mm. A. Front view. B. Rear view. C. From left side. $\times 1.5$.

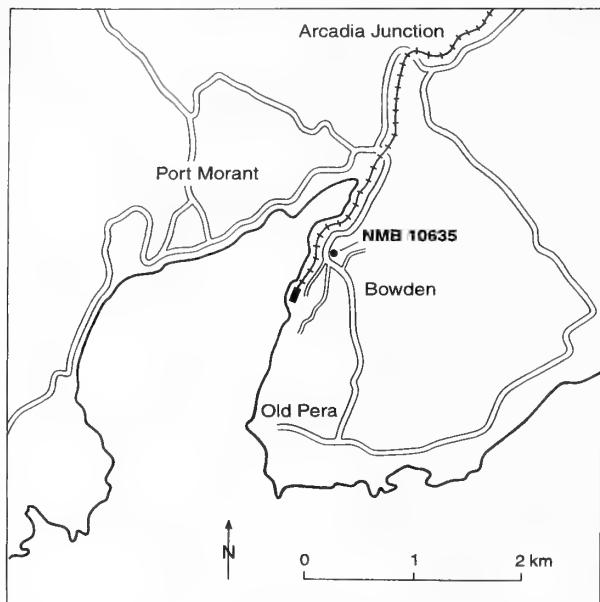


Figure 37. Map of the Port Morant area, southeastern Jamaica, showing NMB locality 10635, where *S. sp. E* has been found (for general location see number 17 of Figure 1).

ented wrinkles near the adapical end of the aperture. Stromboid sinus near the abapical end of the aperture rather shallow. Base of columella bent backward.

Holotype: NMB H 17854 (Figure 25A–D).

Dimensions of holotype: Height 64.4 mm; width 48.8 mm.

Type locality: NMB locality 18677 (= PJ 2214 = PPP 02178); north coast of Escudo de Veraguas, Bocas del Toro, Panama; 1 km east of Long Bay Point. Escudo de Veraguas Formation (late Pliocene). See Figure 25.

Remarks: The holotype and only specimen is fairly complete. The protoconch, the adapical part of the outer lip, and the extreme base are missing. In addition, a good portion of the dorsal surface is strongly corroded, thus leaving the spiral row of knobs on the dorsal part of the body whorl—the diagnostic feature of the subgenus *Lentigo*—not clearly recognizable.

Comparisons: With the exception of a fragment from Cayo Agua identified as *S. cf. fetus*, *S. fetus* is not related to any of the species reported herein. It is stouter and proportionately shorter than any of them, and its apical angle is larger. In this last respect it vaguely resembles *S. lentiginosus*, which, however, is characterized by three to four spiral rows of prominent knobs on the dorsal part of its body whorl, whereas *S. fetus* has two spiral ridges with occasional knoblike elevations.

S. fetus resembles *S. raninus* only superficially. Although the general shape and the apical angle are similar,

the two last knobs on the shoulder of the body whorl are not as developed as the spines in *S. raninus*.

Material: This species is based on a single specimen, the holotype.

Occurrence: Known only from the type locality (Figure 25).

Strombus (Lentigo) cf. fetus Jung & Heitz, sp. nov.

(Figures 23, 26E)

Remarks: A single fragment (NMB H 17855) from Cayo Agua, Panama, is available. It consists of the outer lip (base missing) and a portion of the dorsal side of the body whorl. The whole surface of the fragment is somewhat worn.

Comparisons: This fragment can only be compared to the corresponding part of the holotype of *S. fetus*. The sculpture of the two specimens is almost identical. *S. fetus* has a few more and finer spiral ridges on and above the shoulder. A feature developed in both specimens is a bulge near the outer lip extending parallel to it for some distance.

Occurrence: NMB locality 18734 (= PJ 2271 = PPP 02237). 300 m WNW of Punta Piedra Roja, Cayo Agua, Bocas del Toro, Panama. Cayo Agua Formation, middle Pliocene (early Pliocene according to Dowsett & Cotton, 1996:71, fig. 3.12). See Figure 23.

Strombus (Lentigo) insulanus Jung & Heitz, sp. nov.

(Figures 25, 28A, B)

Etymology: Latin *insulanus* = inhabitant of an island.

Description: Shell reaching a height of about 55 mm, slender. Protoconch and earliest teleoconch whorls not known. Number of preserved teleoconch whorls eight. Sculpture of early teleoconch whorls consists of three varix like axial ribs and two smaller axial ribs in each interspace. These are crossed by six to eight spiral threads. On successive whorls secondary spiral threads appear. On later whorls the spiral threads become subequal in strength, and, at the same time, the axial ribs change their shape into subequal knobs situated on a gradually developing shoulder. There are nine moderately pointed knobs on the last whorl. Dorsal surface of body whorl not preserved, but left side of body whorl clearly shows three spiral rows of small knobs, which—as well as their interspaces—are sculptured by spiral threads. Outer lip not preserved with the exception of its adapical part. Parietal callus smooth. Inner surface of preserved part of outer lip smooth. Base of columella bent backward.

Holotype: NMB H 17842 (Figure 28A, B).

Dimensions of holotype: Height 53.2 mm; width 29.0 mm.

Type locality: NMB locality 18668 (= PJ 2205 = PPP 02169): near the middle of the north coast of Escudo de Veraguas, Bocas del Toro, Panama. Escudo de Veraguas Formation (middle Pliocene). See Figure 25.

Remarks: This species is based on a single specimen, the holotype. It is incompletely preserved: most of the outer lip and the dorsal part of the body whorl are missing, and the dorsal part of the penultimate whorl is damaged. As mentioned above, the protoconch and the earliest teleoconch whorls are not preserved. Despite these unsatisfactory circumstances, we decided that this species should be described formally.

Comparisons: *S. insulanus* is not closely related to any of the species discussed herein with the exception of the form called *S. cf. insulanus* hereafter from the early middle Miocene Grand Bay Formation of Carriacou, Grenadines, Lesser Antilles. Both have a similar sculpture on the early teleoconch whorls, and their apical angle is similar as well. *S. cf. insulanus* is smaller than *S. insulanus* and shows only two (instead of three) spiral rows of knobs on the left side of the body whorl.

Occurrence: Known only from the type locality (see above).

Strombus (Lentigo) cf. insulanus Jung & Heitz,
sp. nov.

(Figures 27, 28C)

Remarks: This species is represented by a single, incomplete specimen (NMB H 17846) from the Grand Bay Formation of Carriacou, Lesser Antilles. Its outer lip and the dorsal part of its body whorl are not preserved, the ventral portion of its penultimate whorl is damaged, and its protoconch and earliest teleoconch whorls are missing.

Similarities and differences between this species, which was listed as *Strombus* sp. by Jung (1971, table 2), and *S. insulanus* are mentioned under the latter.

Occurrence: NMB locality 10703 (= PJ 785): 150 m NW of Point Saint Hilaire, Carriacou, Grenadines, Lesser Antilles. Grand Bay Formation (early middle Miocene) (Robinson & Jung, 1972: 114, 125). See Figure 27.

Further Occurrences of the Subgenus *Lentigo*

So far we have dealt with material that is sufficiently well preserved to be named or to allow the use of open nomenclature. However, there is additional, though scarce, material that cannot possibly be identified specifically. The scarcity of material dictates ignorance of variability. However, it is well known that species of *Strom-*

bus vary considerably. That this applies to species of the subgenus *Lentigo* as well is beautifully documented by the living Eastern Pacific *Strombus (Lentigo) granulatus* Swainson. We have referred to this variability in the discussion of that species.

For reasons of simplicity, the species recorded hereafter are identified by the letters A to E. The majority of these five species are represented by a single specimen.

Strombus (Lentigo) sp. A

(Figures 29, 30)

Remarks: Twelve incomplete specimens from the late Miocene of Falcón, Venezuela are available. They are all not well preserved. One of the figured specimens (Figure 29B) clearly shows two spiral rows of knobs on the dorsal side of the body whorl, the most diagnostic feature of the subgenus *Lentigo*.

Occurrence: NMB locality 17530 (= GS-1-FLCN): 30 m west of the Carrizal Cemetery, a little less than 3 km northeast of La Vela de Coro, Falcón, Venezuela (see Figure 30). Mataruca Member of Caujara Formation (late Miocene); *Globorotalia acostaensis* zone (Díaz de Gamero, 1977:83; see also Jung, 1989:20).

Strombus (Lentigo) sp. B

(Figures 31, 32)

Remarks: Three specimens from the Pliocene of the Valiente Peninsula, Bocas del Toro, Panama are available. Two of them represent spires of juvenile individuals, the third one seems to be an adult shell, the base of which, however, is not preserved.

The protoconch and the earliest teleoconch whorls are not preserved. The earliest preserved sculpture consists of three axial swellings per whorl and four axial ribs in each interspace. These are crossed by 10 spiral threads. On succeeding whorls the axial sculptural elements become subequal in size until they eventually develop into axially elongated knobs of the same size.

On the shoulder of the apparently adult specimen mentioned above there are nine knobs, the last four of which are pointed. The preserved part of the dorsal side of its body whorl carries two spiral rows of knobs.

Occurrence: NMB locality 18716 (= PJ 2253 = PPP 02217): southwest coast of Valiente Peninsula, Bocas del Toro, Panama, 5 km southeast of Cayo Patterson, at south end of Playa Lorenzo (see Figure 32). Very top of Shark Hole Point Formation (Pliocene).

Strombus (Lentigo) sp. C

(Figures 33, 34)

Remarks: A single poorly preserved specimen (NMB H 17858) from the middle or late Miocene of the Paraguaná

Peninsula, Venezuela, is available. The body whorl without the outer lip and a small part of the penultimate whorl are preserved. The shoulder carries nine to 10 knobs, the last five of which are pointed. On the dorsal side of the body whorl there are two spiral rows of knobs.

Occurrence: NMB locality 17526 (= GS-94-PGNA): 200 m south of El Porvenir and 7 km WNW of Pueblo Nuevo, Paraguaná Peninsula, Falcón, Venezuela (see Figure 34). El Porvenir beds (middle or late Miocene, not early Miocene as indicated by Gibson-Smith & Gibson-Smith, 1979:14).

Strombus (Lentigo) sp. D
(Figures 10, 35)

Remarks: A single immature specimen (NMB H 17863) from the Pleistocene of the Burica Peninsula, Panama is available. It consists of seven whorls. The protoconch and the earliest teleoconch whorls are not preserved. It has been collected from the same locality as a specimen of *S. granulatus* (Figures 6E–G, 10) but represents a different species. *S. sp. D* seems to have more teleoconch whorls than *S. granulatus*; it has only eight spiral threads on the early teleoconch whorls as opposed to 11 to 13 in *S. granulatus*. On the last whorl of *S. sp. D* only a weakly developed spiral row of knobs can be recognized which is situated a little distance below the shoulder.

Occurrence: NMB locality 17439 (= PJ 1757): 400 m south of Boca Quebrada Corotú, east coast of Burica Peninsula, Chiriquí, Panama (see Figure 10). Armuelles Formation (Pleistocene).

Strombus (Lentigo ?) sp. E
(Figures 36, 37)

Remarks: A single somewhat immature specimen (NMB H 17864) from the early Pliocene of Jamaica is available. It consists of almost eight teleoconch whorls and a small part of the protoconch. The sculpture of the early teleoconch whorls consists of three axial swellings per whorl and two to three axial ribs in each interspace. All these axial sculptural elements are crossed by eight primary spiral threads on early teleoconch whorls. On succeeding whorls, secondary spiral threads are introduced, and at the same time, the axial swellings and ribs gradually become equal in size. The shoulder of the last preserved whorl carries seven slightly pointed knobs. The edge of the outer lip is not preserved. Its smooth inner surface carries a number of narrow lirae. The base is broken. On the last whorl there is a spiral row of knobs situated a little distance below the shoulder. Additional, more complete material from Bowden is needed to show whether a second row of knobs is developed on the body whorl. For this reason the single available specimen is only tentatively assigned to the subgenus *Lentigo*.

Occurrence: NMB locality 10635: Bowden, Port Morant, Jamaica (see Figure 37). Bowden Formation (early Pliocene).

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Last, but not least, we are grateful to the Kugler Foundation, Basel, for covering the costs of field work, and to the Smithsonian Tropical Research Institute, Panama, for the facilities offered during field work.

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Fine Structure and Distribution of Iridophores in the Photo-Symbiotic Bivalve Subfamily Fraginae (Cardioidea)

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Abstract. Iridophores are widely distributed in the animal kingdom. In bivalves, iridophores occur in photo-symbiotic species belonging to the subfamilies Fraginae and Tridacninae. This paper describes the fine structure and distribution of iridophores in species of Fraginae by light and electron microscopy.

Each iridophore consists of alternating layers of platelets and cytoplasm, both of about 100 nm in thickness, which is the right order for multilayer interference to occur. The iridophores occur in the hypertrophied mantle margin, including tentacles of the postero-dorsal area, and the supra-branchial chamber; these areas are exposed to sunlight when animals keep their valves open and mantle margins expanded. In addition, they also occur in the mantle lining the translucent portions of the posterior valve slope. The occurrence of iridophores appears to correlate positively with the intensity of sunlight reaching the tissues.

The iridophores may function as protectors against harmful sunlight for bivalves. They also may serve to optimize the light intensity for photosynthesis by zooxanthellae.

INTRODUCTION

Many animals have highly reflecting surfaces on various parts of their bodies. In most cases, such high reflectance is the result of thin-film interference from platelets contained in specialized pigment cells called iridophores. Iridophores contain many platelets in the cytoplasm and can reflect light with a wide range of wavelengths (Denton & Land, 1971; Land, 1972).

Among bivalves, brilliant blue or glittering white colors of the hypertrophied mantle margin of giant clams (subfamily Tridacninae; Cardioidea) are interference (structural) colors reflected by dermal iridophores (Kawaguti, 1966). The species of the Tridacninae live in shallow and warm coral reef environments, where short wavelength sunlight is predominant, and have a symbiotic relationship with photosynthetic zooxanthellae (Yonge, 1936). Their mantle margins are widely expanded and contain a great accumulation of zooxanthellae. Based on their ecology, Kawaguti (1966) proposed that the iridophores of Tridacninae might protect against harmful sunlight or supply reflected light for photoreceptive organs located on the wavy mantle margin facing the shell.

Such dermal iridophores also occur in species of Fra-

ginae (Cardioidea). These bivalves are also photo-symbiotic, live in coral reef environments, and contain numerous zooxanthellae (Kawaguti, 1968, 1983; Ohno et al., 1995). The shells of species of Fraginae are usually compressed antero-posteriorly, and are smaller and thinner than those of the Tridacninae. Their mantle margins are not widely expanded beyond the shell margins except for the tentacles (Ohno et al., 1995). Light transmission to the zooxanthellae is facilitated by translucent portions of the posterior slope of the shell. Thus, different areas of the animal receive sunlight in Fraginae than in Tridacninae. The iridophores of the Fraginae may be related to their photo-symbiotic mode of life. However, little is known about the fine structure and distribution or function of iridophores.

This paper describes the fine structure and distribution of iridophores for three species of Fraginae: *Fragum fragum* (Linnaeus, 1758), *Fragum mundum* (Reeve, 1865), and *Corculum cardissa* (Linnaeus, 1758), and provides a sound basis for understanding the function of iridophores for photo-symbiotic bivalves. The evolutionary significance of iridophores among photo-symbiotic species of Fraginae is also discussed.

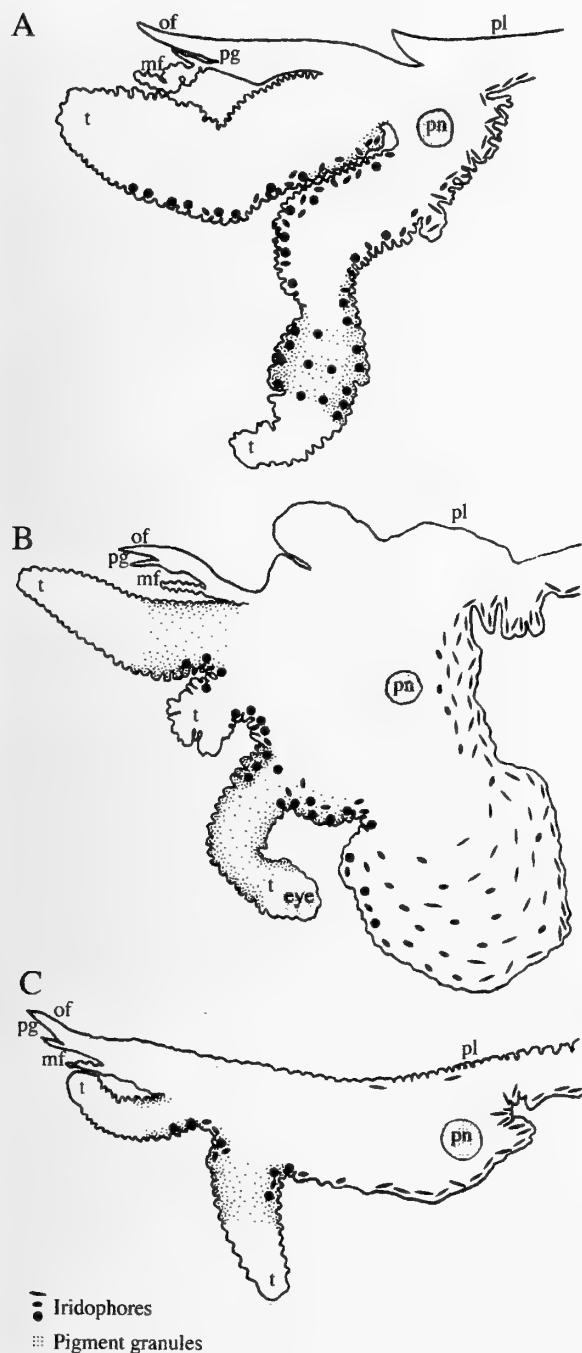


Figure 1. Semi-schematic cross sections of the mantle margin of three species of Fraginace. Three morphological types (disc-shaped, elliptical, spherical) of iridophores and pigment granules are figured. A. *Fragum mundum*. B. *Fragum fragum*. C. *Corculum cardissa*. Key: mf, middle fold; of, outer fold; pg, periostracal groove; pl, pallial line; pn, pallial nerve; t, tentacle. Not to scale.

MATERIALS AND METHODS

Animals were collected on the shallow sand and rocky flats of Bise and Zampa, Okinawa Island, Japan, in September and December 1995.

To study the distribution of iridophores in the mantle margins, specimens of three species (six individuals of *F. fragum*, seven individuals of *F. mundum*, and five individuals of *C. cardissa*) were kept alive in the aquarium at the Natural History Museum and Institute, Chiba. Individuals were observed with a binocular microscope when they expanded their mantle margins and tentacles fully.

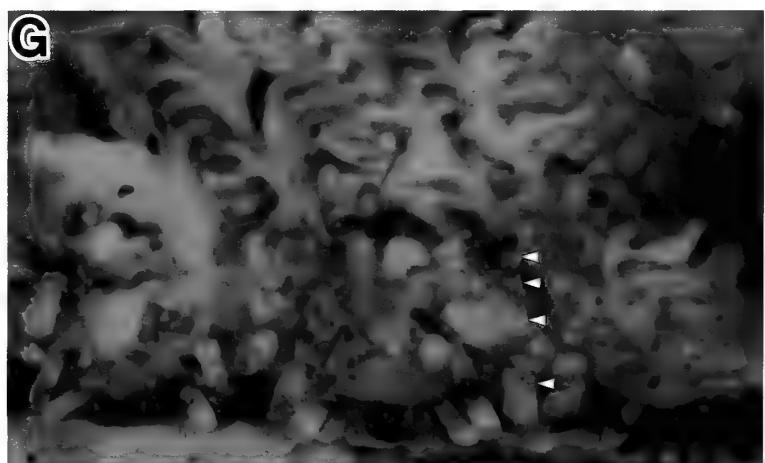
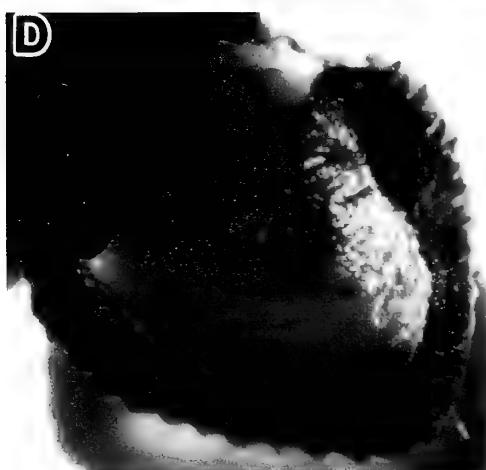
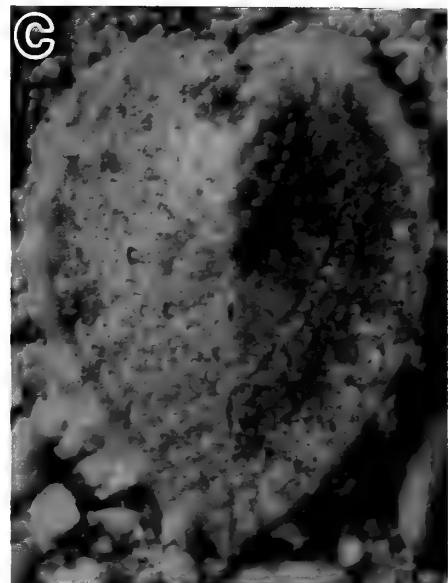
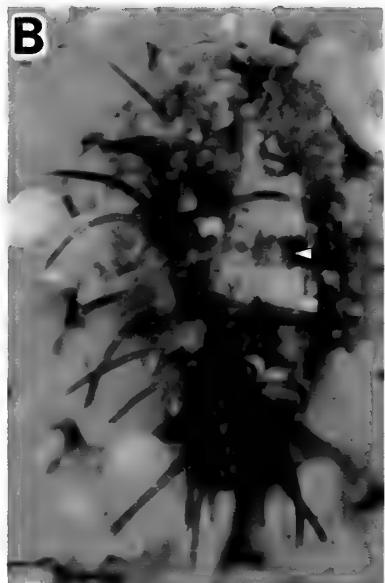
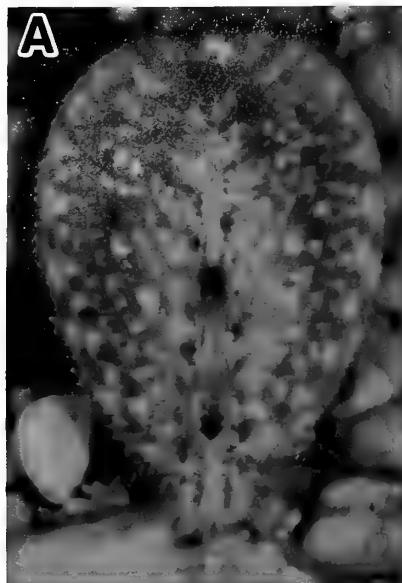
To further study the distribution of iridophores in the mantle lining the shell interior and other soft parts, specimens were fixed without sectioning into small pieces in 2% glutaraldehyde in 0.1 M cacodylate buffer (pH 7.5), and post-fixed in 0.5% osmium tetroxide for 1.5 hours in order to emphasize the contrast between iridophores and other cells. Shells were then slightly decalcified with 4.13% EDTA (pH 7.5) and removed from the soft parts for observation with the binocular microscope.

For transmission electron microscopy (TEM), small pieces (1–2 mm in thickness) were cut from two individuals of *F. fragum*, two individuals of *F. mundum*, and three individuals of *C. cardissa*, and fixed overnight in 2% glutaraldehyde in 0.1 M cacodylate buffer (pH 7.5) with 6% sucrose added for osmolarity. The tissue was then washed in cacodylate buffer for 4 hours and post-fixed in 2% osmium tetroxide for 1.5 hours. After dehydration in an ethanol series, materials were embedded in Epon 812 resin. One- μm -thick sections were cut with a glass knife and stained with toluidine blue for light microscopy. Ultra-thin sections were cut with a diamond knife using an LKB-Ultrotome and stained with uranyl acetate and lead citrate. The sections were examined and photographed with a Jeol JEM-1200EX II TEM.

All the examined specimens are stored in the Natural History Museum and Institute, Chiba (catalog numbers CBM-ZM 114503, 114504, 114505). The taxonomic assignments made in this paper are based on Schneider (1992, 1998).

SHELL FORMS AND LIFE HABITS

The shell forms and life habits of the three species examined differ from each other. *Fragum fragum* attains about 35 mm in PSL (= posterior slope length: umbo to postero-ventral corner). It lives in calcareous, bioclastic sand flats and immerses the valves completely in the sediment. The tentacles secrete mucus, and sand grains adhere to them. In the natural life position of *F. fragum*, only the exhalant and inhalant siphons and a part of the posterior mantle margins covering the shell gape are exposed above the sediment surface (Ohno et al., 1995). This infaunal mode of life results in a clean posterior shell surface with no epibionts.



Fragum mundum is a small (maximum PSL < 10 mm) epifaunal species. It lives in intertidal rocky flats, attaching to algae with mucus, and immerses only the anterior part of the shell in algal mats or shallow sediments. The posterior shell surface is usually covered by epibionts. The shell form of *F. mundum* is similar to that of *F. fragum*, but the former has a more acute angle between the posterior and ventral valve margins.

Corculum cardissa attains about 50 mm in PSL. It is also epifaunal on sand flats. The shell is greatly expanded in width but extremely compressed antero-posteriorly. The posterior shell surface of the specimens living on intertidal sand flats is usually covered by abundant epibionts, whereas those living in subtidal zone have few epibionts.

The shells of the three species are composed of a mosaic of translucent and non-translucent domains. The most translucent domains (windows) are located on the posterior valve slope of each species. In *C. cardissa*, there are various interpretations of the microstructure of the translucent windows proposed by Vogel (1975), Watson & Signor (1986), and Seilacher (1990). Carter & Schneider (1997) reconciled the various interpretations. According to them, the non-translucent domains of the posterior valve slope of *C. cardissa* consist of a fibrous prismatic (FP) outer, branching crossed lamellar (BCL) middle, and irregular complex crossed lamellar (ICCL) inner layers. At the translucent window, the FP outer layer penetrates deeply into the more opaque BCL middle shell layer. Deeper in the windows, such FP structure passes into a dissected crossed prismatic (DCP) structure which forms a planoconvex lens. This modification of the BCL middle shell layer into a more translucent DCP structure is effective to enhance light transmission toward the shell interior (Carter & Schneider, 1997).

In *F. mundum*, the posterior shell windows are as clear as those of *C. cardissa*. The non-translucent domains are milky white in color. Therefore there is high contrast between these two domains. The translucent windows are composed of the needlelike outer crystallites in contrast to the crossed lamellar outer shell layer of the non-translucent domains.

In contrast, the posterior shell windows of *F. fragum* are less translucent than those of the other two species.

The windows are composed of needle-shaped outer crystallites and a complex crossed lamellar inner layer. The needle-shaped outer crystallites radiate, and those of the complex crossed lamellae in the inner shell layer are differently oriented from one lamella subunit to another (Ohno et al., 1995). Thus, light penetrating into the shell of *F. fragum* is scattered by these two layers.

RESULTS

Gross Morphology of the Mantle Margin

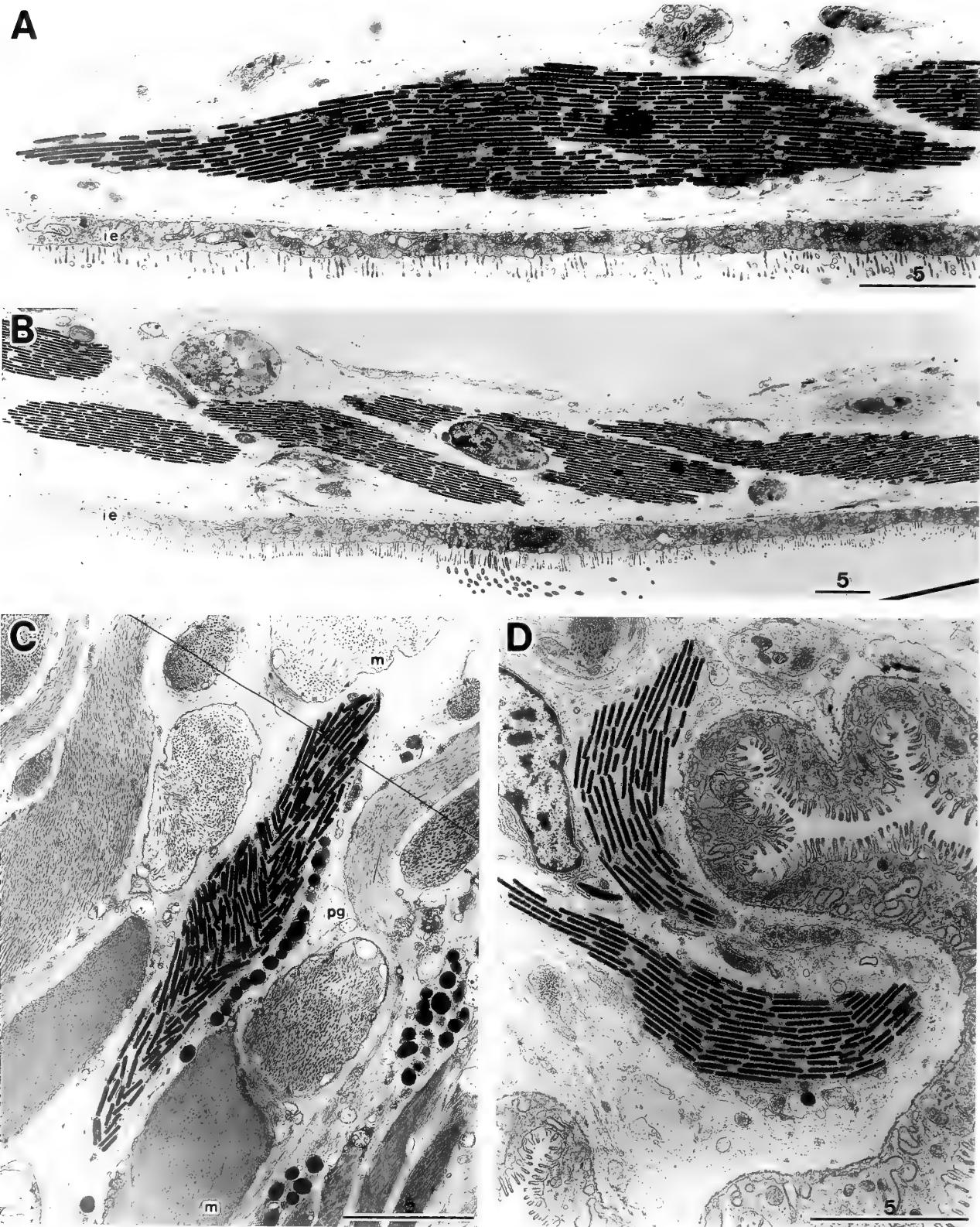
The morphology of the mantle margin was similar in all three examined species. There were three folds at the mantle margins. The outer and middle folds were relatively small; the inner fold, which bore the tentacles, was hypertrophied (Figure 1).

In *F. fragum* and *F. mundum*, the inner fold was furnished with numerous tentacles and was moderately hypertrophied, especially ventral to the inhalant siphon. In *F. fragum*, the tentacles lay somewhat parallel to the surface of the posterior valve slope when they extended fully (Figure 2A), whereas those of *F. mundum* were often expanded at a more or less perpendicular angle to the surface of the posterior valve slope (Figure 2B). In these species, the fully expanded tentacles around the two siphons were as long as the shell width. In addition, these two species widely exposed their hypertrophied mantle margins around the postero-ventral corner of the shell (Figure 2A,B). In contrast, the inner mantle fold of *C. cardissa* was less hypertrophied, and the tentacles were slender and considerably shorter in comparison with their body size. These inconspicuous tentacles extended from the very narrow posterior shell gapes (Figure 2C,G).

Some tentacles around the two siphons of *F. fragum* bore what appeared to be photoreceptive structures; similar structures were not observed in *F. mundum* and *C. cardissa*. The eye-bearing tentacles were more or less shorter than plain tentacles. Mucus cells took the place of the photoreceptive organs in the latter. The photoreceptive structures were composed of lens cells, retinal cells, and ciliated cells. Detailed information on the fine structure of these will be presented in a separate paper.

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Figure 2. Light micrographs showing the iridescent colors reflected by iridophores in living (A, B, C, G) and fixed (D, E, F) specimens. A. *Fragum fragum* (11 mm in PSL), showing red iridescent color in the tentacles. B. *Fragum mundum* (4 mm in PSL), showing red iridescent color penetrating through the translucent window (arrow head). C. *Corculum cardissa* (30 mm in PSL, CBM-ZM 114503), showing few epibionts on the shell surface. D. *F. fragum* (8 mm in PSL, CBM-ZM 114503), showing the accumulation of iridophores in the postero-ventral area of the mantle. E. *F. mundum* (same specimen as in B, CBM-ZM 114504), showing the iridophores located exactly beneath the translucent windows (arrow heads). F. *C. cardissa* (same specimen as in C, CBM-ZM 114505), showing the banded arrangement of the iridophores. G. Enlarged view of posterior edge of *C. cardissa* in C, showing red iridescent color penetrating through the translucent windows. Arrow heads indicate the pigment granules in a tentacle.



Fine Structure of Iridophores

The fine structure of the iridophores was almost identical in the three species. The shape of iridophores showed some variation in relation to their location. Iridophores located in the mantle near the pallial nerve and inside of the pallial line were always disc-shaped, and attained about 50 μm in maximum diameter (Figures 1, 3A, B). Sometimes the shape of these iridophores were slightly modified near the epithelium (Figure 3D). In contrast, iridophores located in the mantle folds, especially in the basal part of the tentacles, were often elliptical to spherical in shape and about 10–15 μm in maximum diameter (Figures 1, 4A, B).

Disc-shaped iridophores contained a stack of 20–30 platelets. Platelets of neighboring stacks were arranged parallel to each other (Figure 3A, B). Each platelet was bound by a double membrane and separated from the next platelets by an approx. 100 nm-thick layer of cytoplasm (Figure 5C). Each platelet was rectangular in shape with truncated or rounded corners (Figure 5B), and measured about 2–3 $\mu\text{m} \times 1\text{--}2 \mu\text{m}$; and was about 100 nm thick. The platelets had an almost uniform electron density, except for occasional platelets in the intermediate stage of organellogenesis that occurred near the nucleus of disc-shaped iridophores (Figure 5A). The nucleus was usually located peripherally; and rough endoplasmic reticula, microtubules, mitochondria, and Golgi bodies were occasionally observed in the disc-shaped iridophores (Figure 5A).

In contrast, in the iridophores located in the tentacles, the platelets were arranged in a somewhat irregular manner (Figure 4A,B). Such an irregular arrangement of platelets sometimes also occurred in disc-shaped iridophores (Figure 3C). No apparent organelles such as nucleus, rough endoplasmic reticulum, or Golgi bodies were observed, nor were intermediate stages of organellogenesis of platelets seen. Isolated platelets were also found extracellularly around the elliptical to spherical iridophores, especially in the tentacles (Figure 4C,D).

Distribution of Iridophores

Iridophores were mainly distributed in the connective tissues beneath the epithelium of the inner mantle fold of the postero-dorsal area. They also occurred in the postero-dorsal area of the supra-branchial chamber. Both the mantle margin and the supra-branchial chamber were observed in living specimens when animals kept their valves open and mantle expanded (Figure 6: dotted area).

In these areas, the iridophores were usually tinged with yellowish brown to red iridescent colors in seawater under fluorescent lighting (Figure 2A). The same distributional pattern of iridophores was found in the three examined species regardless of shell size.

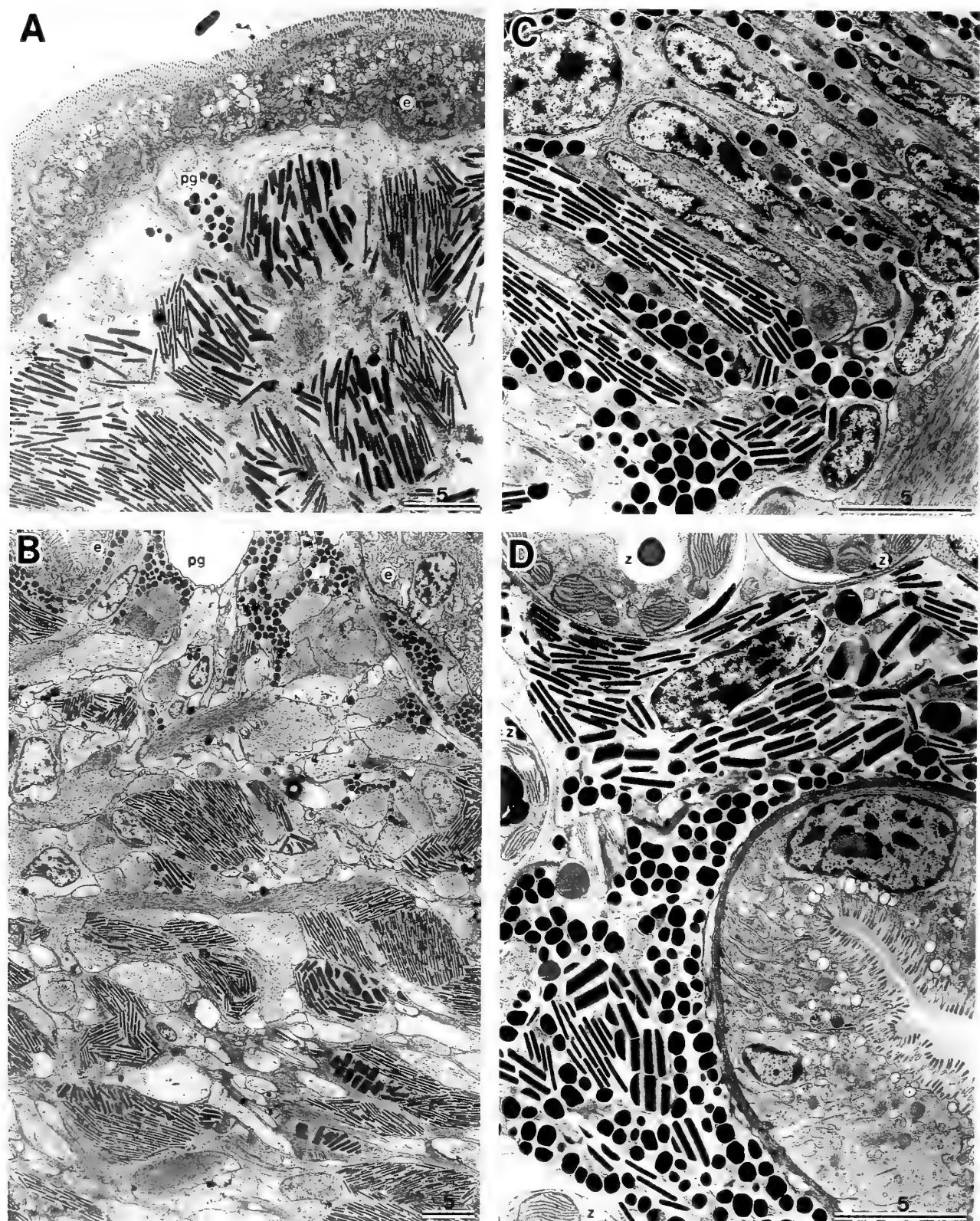
In the mantle margin, the disc-shaped iridophores were most abundantly located at the proximal portion of the inner fold, just beneath the epithelium around the pallial nerve (Figure 1). They were usually arranged parallel to the basal surface of the mantle epithelium (Figures 1, 3D). Large numbers of disc-shaped iridophores were found in the hypertrophied inner fold. These disc-shaped iridophores gradually decreased in abundance toward the tentacles, while spherical iridophores and isolated platelets gradually became more abundant distally in the inner mantle fold (Figure 1). The spherical iridophores appeared to be arranged more or less at random with respect to the basal surface of the mantle epithelium. In the tentacles, they were concentrated basally, but almost absent distally, especially at the tentacle tip (Figure 2A). Only occasional isolated platelets occurred in the distal part of tentacles (Figure 4C,D). These appeared to be a gradual transition from disc-shaped to elliptical and then into spherical iridophores, with an apparent breakdown of cell bodies and release of free platelets at the culmination of this trend.

Iridophores in the tentacles were usually accompanied by numerous pigment granules (= “melanophores” in Kawaguti, 1966). These pigment granules were tinged with whitish silver colors and occurred in distinct bands along the tentacle (Figures 2G: arrow heads). They lay in the connective tissues just beneath the epithelium (Figures 4B, D, 5E). Granules were polygonal and about 0.8 μm in diameter (Figure 5D), and showed almost uniform electron density. Although disc-shaped iridophores were abundant, pigment granules were not observed in the proximal portion of the inner mantle fold (Figure 1).

There were also abundant disc-shaped iridophores in the mantle inside the pallial line of the postero-dorsal area, just beneath the translucent shell windows in some specimens. They were always arranged parallel to the basal surface of the mantle epithelium (Figures 1, 3A, B). The occurrence of iridophores in this area showed variation with shell size and transparency.

Four small specimens of *F. fragum* (5.0, 8.0, 11.0, 11.5 mm in PSL, respectively) examined had iridophores in the mantle inside the pallial line, especially beneath the exhalant siphons. Figure 2D showed numerous irido-

Figure 3. TEM of iridophores in the mantle of *Corculum cardissa* (A, B, C) and *Fragum mundum* (D). A. Disc-shaped iridophore located in the inside of the pallial line. B. Imbricated iridophores located near the pallial line. C. Iridophore surrounded by pallial muscles. D. Iridophores located beneath the inner epithelium near the pallial nerve.
Key: ie, inner epithelium; m, muscle; pg, pigment granules. Scales in micron.



phores occurring in the mantle inside the pallial line lining the posterior valve slope of a small specimen (8.0 mm in PSL). This specimen showed the most dense iridophores in the area among four small specimens, whereas the smallest one (5.0 mm in PSL) had less dense iridophores in the corresponding area than this specimen. In contrast, no iridophores were observed in the mantle inside the pallial line in two larger specimens (14.0, 29.0 mm in PSL). The shells of these larger specimens were much thicker, and their posterior valve slopes were milky white in color and less translucent than those of the smaller ones.

Among *F. mundum* examined (about 4.0 to 6.0 mm in PSL), red iridescent color was observed through a translucent window of the posterior valve slope (Figure 2B). Iridophores were locally restricted to the mantle lining the translucent windows (Figure 2E).

In all specimens of *C. cardissa* examined, iridophores were observed in the mantle lining the posterior valve slope inside the pallial line. Yellowish brown to red iridescent colors were observed through the translucent windows in a small (30 mm in PSL) specimen collected from the subtidal zone (Figure 2C, G). This specimen had abundant iridophores on the posterior slope of the mantle, concentrated in bands that appeared to correspond to the radial ribs on the shell surface (Figure 2F). In contrast, specimens heavily fouled with epibionts had relatively few iridophores, usually restricted to a narrow band along the newly formed shell margin, where epibionts were less abundant than in the older part of the shell. Numerous iridophores also occurred in the mantle lining the anterior side of the shells carina, where the shell was most compressed antero-posteriorly.

Distribution of Zooxanthellae

In all three species examined, zooxanthellae occurred intercellularly in almost all parts of the anatomy. Zooxanthellae were most common inside the shell, especially in the ctenidia, and less common in the exposed parts of the mantle, including the tentacles.

In *F. fragum* and *F. mundum*, zooxanthellae were found in the ventral mantle margins just near the postero-ventral corner. Abundant zooxanthellae also existed within the mantle inside the pallial line along the posterior valve margins and posterior part of the ventral margin. Abundance of zooxanthellae gradually decreased toward the anterior in the mantle. Details of distribution of zoo-

xanthellae in *F. fragum* were described by Ohno et al. (1995).

In contrast to *Fragum* species, *C. cardissa* contained only a few zooxanthellae within the mantle lining the posterior valve slope both outside and inside the pallial line. The mantle lining the anterior valve slope, on the contrary, contained abundant zooxanthellae.

DISCUSSION

Reflecting System of Iridophores

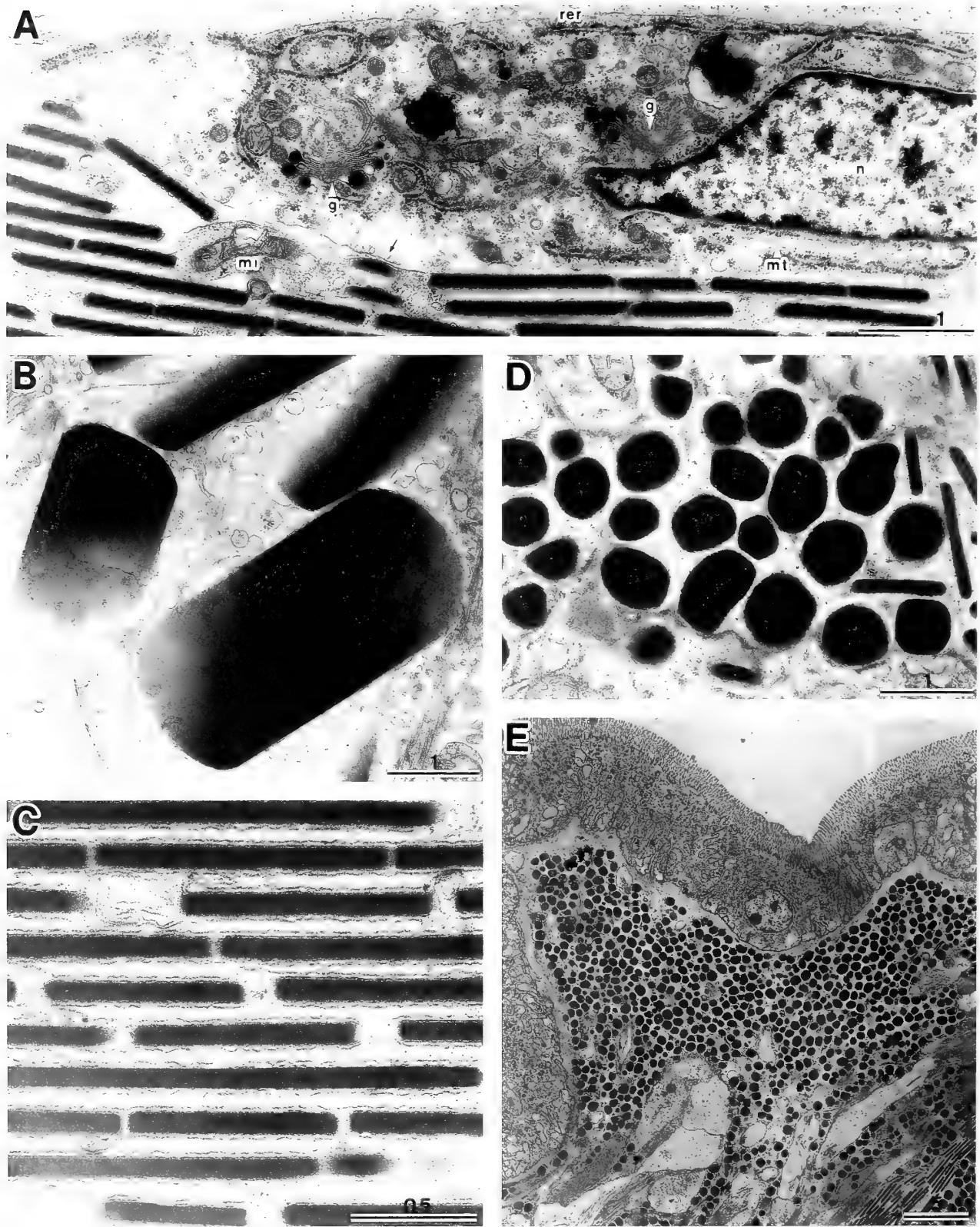
The fine structure of disc-shaped iridophores, such as apparent organella, regular arrangement of platelets, and intermediate stages of organellogenesis of platelets indicates that they represent the initial stage in the differentiation of iridophores. In contrast, an irregular arrangement of platelets in the spherical iridophores and isolated platelets occurring in the distal part of the mantle margin indicates that the spherical iridophores represent the late stages in the development of iridophores, which culminates in cellular degeneration and consequent liberation of platelets. This irregular arrangement of platelets may be a result of their translocation by blood current, i.e., by expansion and contraction of tentacles. Thus, the following discussion focuses on the reflecting system of the disc-shaped iridophores.

The iridophores consist of alternating layers of platelets and cytoplasm, both about 100 nm in thickness, whose refractive indices are high and low, respectively. This thickness is appropriate for multilayer interference to occur. Huxley (1968) showed that the highest reflectivity of a multilayer system at a given wavelength λ_0 would be given if these alternate layers all had an optical thickness of $\frac{1}{4} \lambda_0$. Many biological reflectors, e.g., those found in the integuments and eyes of fish and cephalopods, closely approach such an "ideal" quarter wavelength arrangement (Denton & Land, 1971; Land, 1972).

Assuming that the iridophores examined here are "ideal" quarter wavelength reflectors, the highest reflectivity is calculated from the formula $\lambda_{\text{max}} = 4 n_a d_a$ where n_a is refractive index of platelet and d_a is actual thickness of platelet, which is nearly equal to the thickness of the inter-platelet cytoplasmic layer. Although chemical composition of the platelets of Fraginæ is not examined in the present study, they seem to be composed of chitin or some solid insoluble protein, since they do not shatter or disappear in preparation for electron microscopy as they

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Figure 4. TEM of iridophores located in the tentacles of *Fragum fragum* (A, B) and *Fragum mundum* (C, D). A. Spherical iridophores in the basal part of the tentacle. B. Spherical and irregularly shaped iridophores surrounded by muscles in the basal part of the tentacle. C. Isolated platelets in the distal part of the tentacle. D. Isolated platelets beneath the epithelium of the tentacle. Note the pigment granules in all pictures. Key: e, epithelium; pg, pigment granules; z, zooxanthellae. Scales in micron.



do in both *Pecten* and fish materials, which are composed of guanine (Barber et al., 1967; Denton & Land, 1971; Land, 1972). Taking the refractive index of platelets as those of chitin or dry protein (e.g., keratin): $n_a = 1.56$ (Land, 1972), a peak reflectance is estimated at $4 n_a d_a = 624$ nm. In fact, yellowish brown to red iridescent colors were reflected by iridophores in living specimens (Figure 2A,B,G). This indicates that the multilayer system of iridophores is close to being an “ideal” quarter wavelength reflector.

In all iridophores examined, the platelets were uniform in thickness. Thus, variation in the observed colors must be attributed largely to differences in inter-platelet spacing. Changes in iridescent color from yellowish brown or red in living animals (Figure 2B, G) into greenish yellow following fixation (Figure 2E, F) must be due to shrinkage of inter-platelet space. It can not be attributed to the refractive index of ethanol (1.36), which is close to that of seawater (approx. 1.34). In addition, irregular arrangement of platelets in the spherical iridophores and isolated platelets in the connective tissues results in different reflective colors from those of the disc-shaped ones.

Distribution of Iridophores

Light appears to be the main factor determining the distribution of iridophores in the mantle inside the pallial line.

In *F. fragum*, iridophores were common in the postero-dorsal part of the mantle in small specimens, but absent in the largest specimen examined. In *F. mundum*, iridophores were concentrated in the mantle exactly beneath the translucent windows. In *C. cardissa*, the banded arrangement of iridophores in the posterior half of the mantle was observed in the specimen with few epibionts on the shell surface. Thus, the distribution of iridophores shows good correlation with shell transparency. This suggests that light is an important control in the development of iridophores. It also implies that iridophores may disappear with growth unless they receive the sufficient amount of sunlight.

Functional Significance of Iridophores

Iridophores are distributed in the eyes and the integuments of numerous animals (Denton & Land, 1971; Land, 1972; Bubel, 1984). They invariably have a multilayer structure consisting of alternating layers with high and

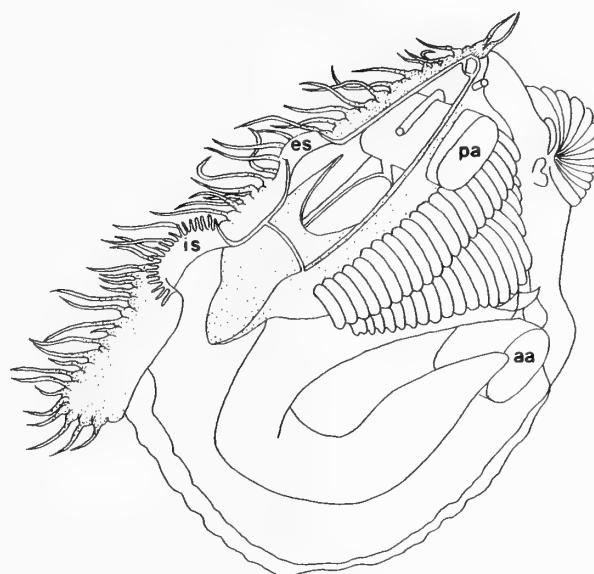


Figure 6. Schematic figure of *Fragum fragum* showing the anatomy and occurrence sites of iridophores (dotted area). Key: aa, anterior adductor muscle; es, exhalant siphon; is, inhalant siphon; pa, posterior adductor muscle. Modified from the text-fig. 2 in Ohno et al. (1995).

low refractive indices. They can serve many functions. Multilayer reflectors, for example, are found in many vertebrate and molluscan eyes as tapetal reflectors (Denton, 1971; Barber et al., 1967). Fish and cephalopods use them as mirrorlike reflectors that serve to camouflage them and provide a display of surface color (Mirow, 1972a, b; Brocco & Cloney, 1980), or serve as reflectors in photophores (e.g., Young & Bennett, 1988).

It is obvious that the iridophores are not involved in changes of body color in species of Fraginae since changes of reflective color in the living animal and physiologically alterable chromatophores are not found.

In the examined species of Fraginae, neither photoreceptive organs nor photophores were observed in *F. mundum* and *C. cardissa*. Although *F. fragum* had eyes in the tip of the tentacles, no iridophores were present within or around them. Therefore it is also clear that the iridophores are not involved in photoreception and luminescence.

Kawaguti (1966) proposed the idea that the iridophores located in the expanded mantle of the giant clam *Tridacna gigas* (Linnaeus, 1758) reflect the sunlight to eyes on

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Figure 5. TEM of iridophores and pigment granules of *Corculum cardissa* (A, C), *Fragum fragum* (B, E), and *Fragum mundum* (D). A. Intermediate stage of organellogenesis of iridosomal platelets (arrow) near the nucleus. B. Horizontal section through platelets. C. Vertical section through a stack of platelets of the disc-shaped iridophore. D. Pigment granules in the tentacle. E. Accumulation of pigment granules beneath the epithelium of the basal part of tentacle. Key: g, Golgi body; mi, mitochondria; mt, microtubule; n, nucleus; rer, rough endoplasmic reticulum. Scales in micron.

the mantle margin and this may facilitate the animals response to changes of brightness in the environment. This possible role does not apply here because the iridophores located in the tentacles are fewer than those of the giant clam and are usually covered by sand grains in *F. fragum*.

Although the species examined lack an association between iridophores and photoreceptive organs, *Cerastoderma edule* (Linnaeus, 1758) of the closely related subfamily Lymnocardiinae has iridophores in the tentacle eyes. Barber & Wright (1969) revealed that the iridophores of *C. edule* function as photoreceptive reflectors. The shape of platelets in the iridophores of *C. edule* is similar to those of Fraginae. This resemblance may be due to a similar chemical composition of the platelets in the two groups. It is noteworthy that these closely related groups evolved the same type of iridophore for different functions.

There is a general agreement that the postero-dorsal shell of the Fraginae became translucent to supply light for zooxanthellae (Watson & Signor, 1986; Ohno et al., 1995; Carter & Schneider, 1997). However, such shell transparency may result in an oversupply of harmful light to bivalves. Judging from the distribution of iridophores within the mantle inside the pallial line, it seems that the penetration of light in translucent portions of the shell is effectively reduced by reflection of iridophores. Thus, the prime function of iridophores may be to reflect excessive and harmful light in the tropical coral reef environments, where short wavelengths predominate. This reflection may allow the optimal amount of light to reach the bivalves.

However, such a screening effect by the iridophores may be disadvantageous for the photosynthesis of zooxanthellae. Zooxanthellae need sufficient light for photosynthesis. However, zooxanthellae were not concentrated in the mantle just beneath the translucent shell windows but occurred in the gill leaflets where iridophores were not observed. Moreover, in *C. cardissa*, which had the most translucent shell, zooxanthellae were most common in the anterior mantle, i.e., farthest from the impinging light; the accumulation of zooxanthellae is not common in the brightest area within the mantle. This phenomenon might be explained by "shade adaptation" of zooxanthellae, meaning molecular level adaptation to enable photosynthesis in low light intensity (Falkowski & Owens, 1980). Ohno et al. (1995) reported that the compensation point of photosynthesis of the zooxanthellae of *F. fragum* is one-quarter that of the zooxanthellae of the epifaunal *Tridacna maxima* (Röding, 1798) (Scott & Jitts, 1977), and indicated shade adaptation for the zooxanthellae of *F. fragum*. It seems reasonable therefore to suppose that this shade adaptation of zooxanthellae influenced the distribution of zooxanthellae within the soft parts of Fraginae.

Another explanation for zooxanthellae to avoid living in a brightly lit area is to reduce the impact of harmful

ultraviolet radiation. Gleason & Wellington (1993) reported that increased ultraviolet radiation in clear water induced coral bleaching (the loss of zooxanthellae) at depths greater than 20 m in the absence of abnormally high seawater temperatures. At such depths, zooxanthellae living within the coral reported by them may be shade-adapted species. Thus, it is likely that shade-adapted zooxanthellae avoid not only high light intensity but also ultraviolet light. It is also likely that iridophores may provide possible screening against ultraviolet light as well as optimize light intensity, and thus provide shade-adapted zooxanthellae of Fraginae with a more light-protected environment.

This screening effect has been demonstrated by Kawaguti (1966) for the iridophores of the giant clams (*Tridacna*). In the case of giant clams, the iridophores are associated with a great accumulation of zooxanthellae in the hypertrophied mantle. Such differences in the mode of association between iridophores and zooxanthellae in the Fraginae and Tridacninae might be due to the different ability of photosynthesis of the symbiotic zooxanthellae.

Additionally, the distal part of the tentacles had almost no iridophores in spite of their exposure to high irradiance. In this area, numerous polygonal pigment granules were located beneath the outer epithelium, which may play the role of protection against harmful sunlight instead of iridophores. In fact, the tentacles of living specimens were whitish silver in color because of the light scattered by the pigment granules.

Concluding Remarks

Regulation of light supply by refraction and scattering in the soft parts to protect the health of the animal is a plausible function of the iridophores in the Fraginae. It is also likely that regulatory effect provides optimum light supply for the photosynthesis of zooxanthellae.

Ohno et al. (1995) proposed that the photo-symbiosis in the Fraginae was initiated by the association of shade-adapted zooxanthellae and an ancestral infaunal bivalve. Because of such a point of view, a comparison with an infaunal Fraginae *Fragum unedo* (Linnaeus, 1758) may be helpful. Interestingly, the shell of *F. unedo* is not translucent, although the species is photo-symbiotic. Such a non-translucent shell seems to retain the ancestral form of the Fraginae. *F. unedo* has hypertrophied mantle margins containing many iridophores, and exposes them widely on the sediment surface to collect light (Kawaguti, 1983; Ohno et al., 1995). This association of a photo-symbiotic infaunal bivalve having a non-translucent shell and iridophore indicates that an ancestral bivalve of the Fraginae had iridophores in the exposed soft parts. It is likely, therefore, that iridophores have developed in order to regulate the light supply to the soft parts in the early history of a photo-symbiotic relationship between the Fraginae and zooxanthellae.

Since photo-symbiosis was established, photosynthesis of zooxanthellae may have worked as a selective agent that would have favored an effective light supply. In order to establish the effective light supply without risking predation, transparency of the shell may have developed. Moreover, the iridophores may have increased their important role as regulators of the light both for the bivalve itself and the zooxanthellae.

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Taranidaphne dufresnei (Mollusca: Gastropoda: Turridae), New Genus and Species from Yemen, Red Sea

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Abstract. Based on specimens from the Museo di Zoologia dell' Università di Bologna, *Taranidaphne dufresnei* gen. & sp. nov. is here described from Yemen, Red Sea and Gulf of Aden. The new genus is compared to *Taranis* Jeffreys, 1870, which it resembles mainly in apertural features. A total of four recent species are at present included in the genus. A redescription of *Daphnella (Pleurotomella) amphitrites* Melvill & Standen, 1903, and notes on *Daphnella (Pleurotomella) nereidum* Melvill & Standen, 1903, species assigned to the new genus and originally described from the Gulf of Oman, are included. *Bela erythraea* Jousseaume, 1895, from Atacka, Suez, Red Sea, is here regarded as a synonym of *Pleurotoma (Bela) hongkongensis* Sowerby, 1888, from Hong Kong, a species also referred to *Taranidaphne*. The lectotype and a paralectotype of *Bela erythraea* are figured. A lectotype for *Daphnella (Pleurotomella) amphitrites* is designated and figured; syntypes of *Pleurotoma (Bela) hongkongensis* and *Daphnella (Pleurotomella) nereidum* are figured for the first time.

INTRODUCTION

During the examination of turrid samples dredged by the French oceanographic ship *Marion Dufresne* offshore Yemen, Red Sea and Gulf of Aden (Red Sed '92 European Community Project, September 1992, Gulf of Aden and South Red Sea) few adult specimens and several fragments of *Daphnella (Pleurotomella) amphitrites* Melvill & Standen, 1903, and a very distinctive, unknown turrid species were found. These species prove to belong to an undescribed, widely distributed genus represented by a few species.

In this paper the traditional classification of the family Turridae is used rather than that proposed by Taylor et al., 1993. Although this proposed classification is the first largely based on anatomical characters, Rosenberg (1998) has recently demonstrated that their results cannot be reproduced.

Abbreviations: a/l = ratio of aperture length to total shell length; b/l = ratio of shell breadth to total length; BMNH = The Natural History Museum, London; HUJ = Hebrew University, Jerusalem; MNHN = Muséum National d'Histoire Naturelle, Paris; MZB = Museo di Zoologia dell'Università di Bologna; NMSA = Natal Museum, Pietermaritzburg.

TAXONOMY

Family TURRIDAE H. & A. Adams, 1853

Subfamily DAPHNELLINAE Deshayes, 1863

Genus *Taranidaphne* Morassi & Bonfitto, gen. nov.

Type species: *Taranidaphne dufresnei*, sp. nov.

Description: Shell thin and small (up to 8 mm in length), fusiform-biconic to broadly-biconic in shape, teleoconch with a small to intermediate number of rapidly expanding whorls, apex acute, last whorl large and inflated. Whorls often distinctly shouldered/keeled. Suture deep. Subsutural ridge present, often bisected by a groove, with laterally projecting nodules. Aperture lanceolate to oblong-oval. Parietal wall gently convex. Columella convex at base. Labial callus very thin or absent. Outer lip thin, devoid of denticles, not preceded by a labral varix. Stromboid notch absent or very slight. Anal sinus resembling that of *Taranis*, i.e., very shallow and broad, with its apex on periphery. Siphonal canal very short and broad, poorly differentiated from aperture and lacking a terminal notch. Base moderately concave on left side. Sculpture consisting of collabral axial ribs, rather straight below periphery, prosocline above it, crossed by sharply incised spiral ridges to form axially aligned nodules. Interstices quadrangular in shape. Protoconch multispiral or paucispiral, with

diagonally cancellate sculpture or granulose spiral threads. Teleoconch translucent white; protoconch yellowish in fresh specimens.

Discussion: *Taranidaphne* superficially resembles *Taranis* Jeffreys, 1870, a very widely distributed genus (Kilburn, 1991; Powell, 1967), recently referred to the monotypic subfamily Taraninae Casey, 1904 (Kantor & Sysoev, 1989; Taylor et al., 1993). These genera have the same number of teleoconch shell whorls, type of anal sinus (very shallow and broad, with its apex on periphery) and other apertural features (length of siphonal canal, absence of ornament on the outer lip and columella). However, *Taranidaphne* bears a strongly developed sculpture of sharply incised spiral ridges which cut collabral axial ribs to form conspicuous axially elongated squares with quadrangular interstices. In *Taranis* the sculpture is much fainter, consisting of imbricate axial riblets/lamellae crossed by spiral lirae to form at most minute nodules. *Taranidaphne* further differs from most species allocated in *Taranis* in possessing a thicker, more produced, and less excavated base. The species included in the new genus are larger than those of *Taranis*, which are minute, with most species not exceeding 4.6 mm in maximum length.

Under SEM, the examined species of *Taranidaphne* proved to be devoid of the microscopic granules which are typically present in *Taranis* (Bouchet & Warén, 1980; Kilburn, 1991). Finally, whereas the shell of *Taranis* is frequently colorless, that of the new genus is often bicolored (crystalline white teleoconch, yellowish protoconch).

The Atlantic bathyal *Taranis malmi* (Dall, 1889) bears a protoconch which closely resembles that of *Taranidaphne*, being multispiral and diagonally cancellate (Bouchet & Warén, 1980). However, due to its high spire and very different apex, its position within *Taranis* has been questioned by Kilburn (1991), who suggested the German Miocene daphneline genus *Magnella* Dittmer, 1960, as a better option. The present authors have not studied the type species of the latter but, judging from the description and figure given by Powell (1966), consider this possibility reasonable. However, *Taranidaphne* differs widely from *Magnella* in its much lower spire, strongly inflated body whorl, absence of microscopic spirally aligned granules and cytharidlike axials on teleoconch whorls.

Apart from the species described below, the new genus at present includes: *Daphnella (Pleurotomella) amphitrites* Melvill & Standen, 1903, *D. (Pleurotomella) nereidum* Melvill & Standen, 1903, two deep-water taxa described from the Gulf of Oman, and *Pleurotoma (Bela) hongkongensis* Sowerby, 1888, from Hong Kong, China Sea (=*Bela erythraea* Jousseaume, 1895 from Atacka, Suez, Red Sea).

Presently, the authors, in the absence of anatomical evidence and despite a superficial resemblance to *Taranis*

in apertural features, prefer to allocate the new genus to the subfamily Daphnellinae rather than Taraninae. The presence within *Taranidaphne* of species with a diagonally cancellate protoconch, a character currently considered diagnostic of Daphnellinae (Powell, 1966; Taylor et al., 1993) is consistent with the proposed assignment.

It should be noted that Taylor et al., 1993 conserve the monotypic subfamily Taraninae Casey, 1904, only with doubt because *Taranis* differs considerably in shell characters from any other turrid group lacking a radula. However, both *Magnella* and *Taranidaphne* so closely approach *Taranis* in several shell characters that a profound taxonomic distinction based solely on shell characters would certainly be rather doubtful.

Range: Red Sea, Gulf of Aden, Gulf of Oman, and China Sea.

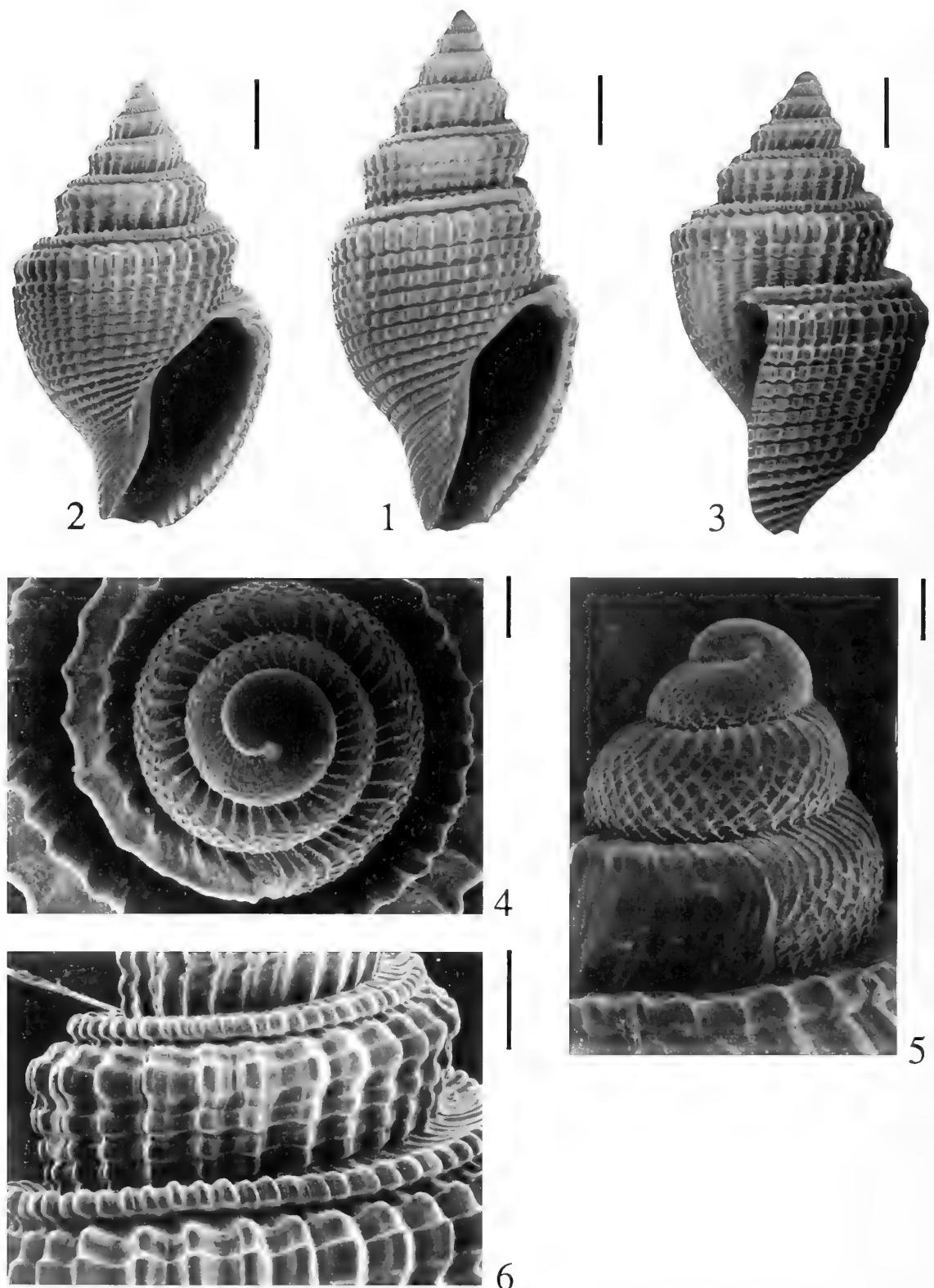
Etymology: from *Taranis* + *Daphnella*, gender feminine. Referring to the resemblance to these genera in apertural features and protoconch respectively.

***Taranidaphne dufresnei* Morassi & Bonfitto,
sp. nov.**

(Figures 1–6)

Diagnosis: Shell up to 6.5 mm in length, fusiform-biconic to broadly biconical. Teleoconch whorls strongly shouldered above median, sculptured by deeply incised spiral ridges crossing narrower collabral axial ribs forming squares. Sutural channel very wide and deep. Aperture oblanceolate. Siphonal canal very short. Anal sinus broad and shallow. Color white; protoconch yellowish. Protoconch of 3–3.5 whorls, with diagonally cancellate sculpture.

Description: Shell small, thin, fusiform-biconic to broadly biconical with orthoconoid spire, acute apex and large, inflated last whorl. Base well produced, curving only slightly to left. Teleoconch consisting of 4.25–5 rapidly expanding whorls, strongly and angularly shouldered above mid whorl. Sutural channel very wide and deep. Left side of base concave, without fasciole. Aperture broad, oblanceolate, with greatest width at posterior third, slightly bent at siphonal canal. Parietal wall slightly convex, columella gently convex. Labial callus a thin glaze. Outer lip very thin, devoid of denticles and not preceded by a labial varix. Siphonal canal short and broad, poorly differentiated from aperture with its termination slightly obliquely truncate, lacking a terminal notch. Anal sinus very shallow and broad with its apex on periphery. Stromboid notch absent. Sculpture consisting of flat-topped spiral ridges with deeply incised and narrower to subequal intervals crossing thin axial ribs to form strong, axially elongated squares. Axials narrower than their intervals, rather orthocline below the shoulder angulation, forming raised and prosocline plicules on sutural channel.



Figures 1–6. *Taranidaphne dufresnei* Morassi & Bonifitto, sp. nov. Figure 1. Holotype, MZB 12913; scale bar 1 mm. Figures 2, 3. Paratype from Gulf of Aden, MZB 12914; scale bar 1 mm. Figures 4, 5. Protoconch, MZB 12918; scale bar 100 μ m. Figure 6. Teleoconch whorls, MZB 12914; scale bar 500 μ m.

First teleoconch whorl with a narrowly channelled suture, a subsutural lira, and a peripheral keel above mid whorl, crossing axials to form laterally projecting nodules. Second whorl with a distinct subsutural ridge bearing axially elongated, coglike nodules, a stronger keel, and two spiral ridges anteriorly. At this stage, the axial ribs have almost completely been cut into elongated squares, while the sutural channel has become very wide and distinctly concave, the shoulder slope reduced to a narrow, deep groove between the previous subsutural ridge and the periphery. On the third whorl the shoulder keel has a primary row of squares, and, according to specimens, a much weaker row adapically, or one row on either side of it. Below the keel, there are three spiral ridges on this and the subsequent whorl; four to five on the last whorl. Body whorl with 35–46 axial ribs evanescent below periphery. Base of body whorl with 13–16 spiral ridges, interstices much narrower than spirals. Teleoconch translucent white; protoconch yellowish (in fresh specimens). Protoconch multispiral, conical, consisting of 3–3.5 strongly convex whorls; the first small and rounded, covered with minute spiral threads cutting finer axial threads, giving a somewhat reticulate appearance; subsequent whorls with about 80 opistocyst axial riblets crossed by oblique threads to form a diagonal cancellation resulting in numerous lozenges on 75% of the whorl. Under SEM, the surface is seen to bear dense, divaricating spiral microstriae. Protoconch diameter: 0.40–0.45 mm.

Measurements (in mm):

	Length	Breadth	Aperture	b/l	a/l
Holotype	6.5	3.2	3.0	0.49	0.46
Paratypes	4.8–6	2.5–3.4	2.5–3	0.52–0.57	0.50–0.52

Type locality: Offshore Yemen, Red Sea (14°46'72"N, 42°32'82"E), 76 m depth on muddy sand.

Type material: Four adult specimens (bored), three juvenile, and 14 fragments from the type locality; two adult specimens from Gulf of Aden (12°02'36"N, 44°29'53"E), 1400 m depth.

Holotype: MZB 12913

Paratypes: Two from Gulf of Aden MZB 12914–15, 16 from Red Sea MZB 12916–31; one BMNH; one HUJ, MNHN; one NMSA.

Etymology: Named after the French oceanographic ship, *Marion Dufresne*, which dredged the available material.

Discussion: *Taranidaphne dufresnei* sp. nov. differs distinctly from other members of the genus, notably in the presence of strong axially elongated squares, a very wide sutural channel, and a not bisected subsutural ridge.

Two forms of this distinctive species occur, namely a

fusiform-biconic one and a shorter, more biconical morph. Apart from the difference in teleoconch shape, the latter differs from the former in possessing a half whorl more in the protoconch and fewer teleoconch whorls (about 4.25 instead of 5). Such variability is presumably not depth-related because both forms occurred at the same station (14°46'72"N, 42°32'82"E), but is probably indicative of dimorphism within the species.

The broad morph of *T. dufresnei* may resemble some species allocated in the widely distributed daphneline genus *Mioawateria* Vella, 1954. However, members of that genus are even more broadly biconical in shape, with a lower spire and a thicker shell.

We are inclined to consider the occurrence of *Taranidaphne dufresnei* at 1400 meters depth (12°02'36"N, 44°29'53"E) as merely accidental, the result of transport from the continental shelf.

***Taranidaphne amphitrites* (Melvill & Standen, 1903), comb.nov.**

(Figures 7–11, 12)

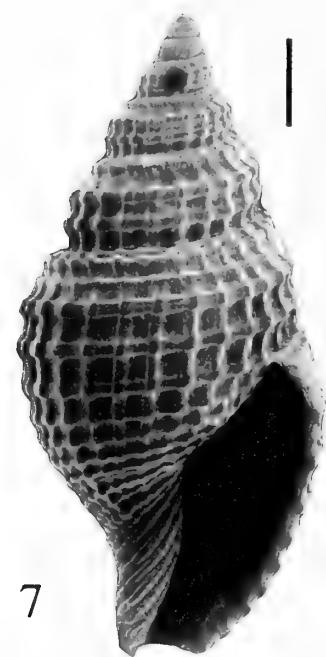
Daphnella (Pleurotomella) amphitrites Melvill & Standen, 1903:316, pl. XXIII, fig. 3.

Type locality: Gulf of Oman, 24°58'N, 56°54'E, 156 fathoms.

Pleurotomella amphitrites (Melvill & Standen), Melvill, 1917:196.

Diagnosis (Yemen specimens): Shell up to 6.8 mm in length, fusiform-biconic. Teleoconch whorls not distinctly shouldered or keeled, sculptured by deeply incised spiral ridges crossing collabral axial ribs forming nodules. Suture narrowly channelled, subsutural ridge bisected by a groove. Aperture somewhat lanceolate. Siphonal canal very short. Anal sinus broad and shallow. Color white; protoconch yellowish. Protoconch papilliform of two whorls, with diagonally cancellate sculpture.

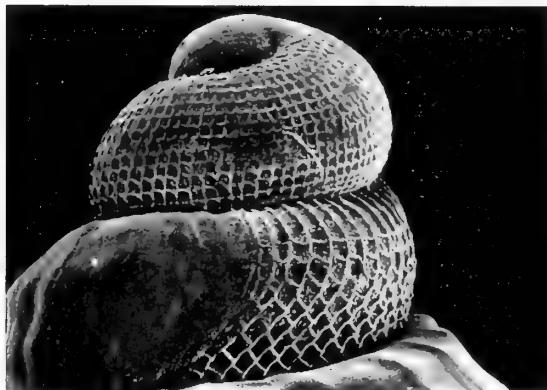
Description (Yemen specimens): Shell small, thin, fusiform-biconic with a rather acute, orthoconoid spire and inflated body whorl. Base well produced curving strongly to left. Teleoconch whorls about five with deep, narrowly channelled suture. Whorls convex, not distinctly shouldered or keeled. Left side of base moderately convex. Aperture somewhat lanceolate with greatest width at posterior third, moderately strongly bent at siphonal canal. Parietal wall moderately convex. Columella sinuous and convex, narrow and acuminate anteriorly. Labial callus absent. Outer lip thin, very convex, devoid of denticles, not preceded by a labial varix. Siphonal canal poorly differentiated from aperture, not deeply notched. Anal sinus almost imperceptible, with its apex on periphery. Stromboid notch feeble but present. Sculpture consisting of flat-topped spiral ridges with deeply incised and much broader intervals crossing thin axial ribs to form small, axially aligned nodules. Axials equal to intervals or half their



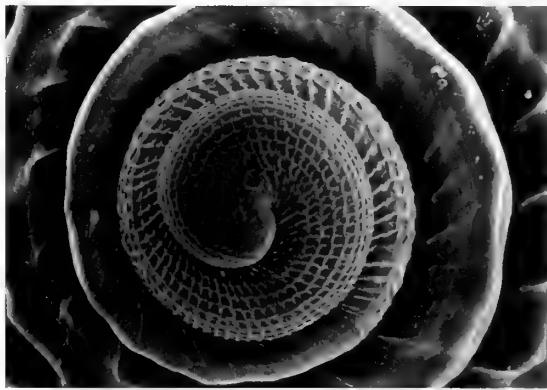
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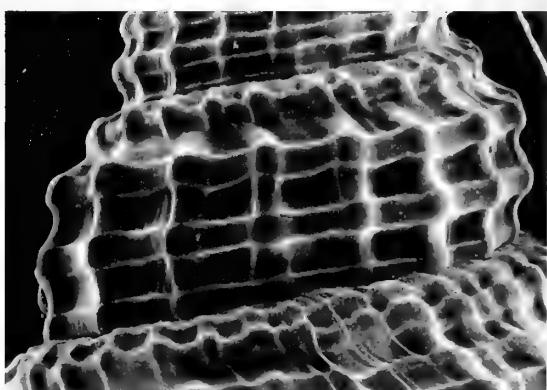
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11

Figures 7–11. *Taranidaphne amphitrites* (Melvill & Standen, 1903). Figures 7, 8. Specimen from Yemen (Red Sea), MZB 12932; scale bar 1 mm. Figures 9, 10. Protoconch, MZB 12937; scale bar 100 μm . Figure 11. Teleoconch whorls, MZB 12933; scale bar 500 μm .

width, rather straight below the peripheral ridge, arcuate and prosocline above it. Interstices broad, quadrangular. First teleoconch whorl with a nodulous subsutural lira, a peripheral keel, and a weaker ridge anteriorly. Subsequent whorls with a bisected subsutural ridge rendered nodulous

by axial ribs, two main spiral ridges, and a weaker one just above the abapical suture. Body whorl with one spiral lira on shoulder slope and, according to specimen, one spiral lira in each interval between the three main ridges. Body whorl with 30–33 axial ribs, evanescing at level of

parietal-columellar junction. Base of body whorl with 15–16 spirals with narrower intervals. Teleoconch translucent white, protoconch yellowish (in fresh specimens). Protoconch papilliform of two whorls; first tilted and covered with minute and dense spiral threads crossed by finer axial threads, giving a reticulate appearance; subsequent whorl developing a diagonally cancellate sculpture of opisthocyst axials crossed by oblique riblets in abapical two-thirds of the whorl. Protoconch diameter: 0.36–0.45 mm.

Measurements (in mm):

	Length	Breadth	Aperture	b/l	a/l
Specimen 1	6.1	2.9	3.1	0.48	0.51
Specimen 2	6.8	3.3	3.4	0.49	0.50
Specimen 3	6.4	3.3	3.3	0.52	0.52

Material examined: Two syntypes of *Daphnella (Pleurotomella) amphitrites* in BMNH (reg. no 1903.12.15.40–41), one marked with a red dot is most probably the figured specimen and is here designated as lectotype, 6.8 × 3.2 mm.; three adult specimens (MZB 12932–34), two juveniles (MZB 12935–36), and eight fragments (MZB 12937–44) from Yemen, Red Sea (14°46'72"N, 42°32'82"E), 76 m depth on muddy sand.

Remarks: The available material has been identified as *Daphnella (Pleurotomella) amphitrites* Melvill & Standen, 1903, after comparison with the two syntypes of the species stored in BMNH. *Taranidaphne amphitrites* much more closely resembles *Taranidaphne hongkongensis* (Sowerby, 1888) than any other member of the genus. The only significant difference we can define is the protoconch sculpture which in *T. hongkongensis* is of granular spiral threads, whereas in *T. amphitrites* it is diagonally cancellate.

***Taranidaphne nereidum* (Melvill & Standen, 1903), comb. nov.**

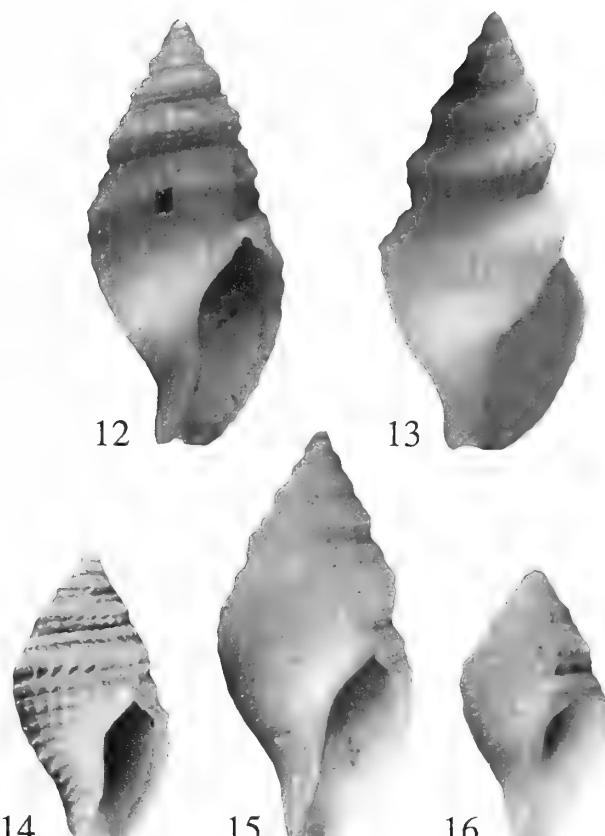
(Figure 13)

Daphnella (Pleurotomella) nereidum Melvill & Standen, 1903:315, pl. XXIII, fig. 2.
Type locality: Gulf of Oman, 24°58'N, 56°54'E, 156 fathoms.

Pleurotomella nereidum (Melvill & Standen), Melvill, 1917: 197.

Material examined: Two syntypes of *Daphnella (Pleurotomella) nereidum* stored in BMNH (reg.no. 1903.12.15.83).

Notes: Shell small and thin, biconic with orthoconoid spire, acute apex, and inflated body whorl. Base well produced curving distinctly to left. Teleoconch consisting of 5.25 rapidly expanding whorls strongly angulated at mid whorl by a keel. Suture deep, narrowly channelled. Left side of base deeply concave, without fasciole. Aperture



Figures 12–16. Figure 12. Lectotype of *Daphnella (Pleurotomella) amphitrites* Melvill & Standen, 1903, BMNH 1903.12.15.40. Figure 13. Syntype of *Daphnella (Pleurotomella) nereidum* Melvill & Standen, 1903, BMNH 1903.12.15.83. Figure 14. Syntype of *Daphnella (Pleurotomella) hongkongensis* Sowerby, 1888, BMNH 1889.2.1.9–10. Figures 15, 16. Lectotype and paralectotype of *Bela erythraea* Jousseaume, 1895, MNHN.

broad oblanceolate, with greatest width at posterior third, strongly bent at siphonal canal. Parietal wall convex, columella strongly convex. Labial callus absent. Outer lip thin, devoid of denticles, not preceded by a labral varix. Siphonal canal short, with its termination obliquely truncate, lacking a notch. Anal sinus almost imperceptible, with its apex on peripheral keel. Shoulder slope strongly declivous. Sculpture consisting of thin, collabral axial ribs, narrower than their intervals, crossed by spiral ridges, of which the peripheral one forms a prominent keel, to form axially aligned squares. Peripheral keel at one-third of whorl below the suture on early teleoconch whorls, median on latter. First teleoconch whorl with a very feeble subsutural lira and the peripheral lira crossed by axials to form nodules. Subsequent whorls with two main spiral ridges below the median keel. Subsutural ridge distinctly bisected. Penultimate whorl with a bisected subsutural ridge, two spiral threads on shoulder slope, a well developed peripheral keel, and two main

spiral ridges anteriorly. Body whorl with 19 spiral ridges, 12 of which are on base. Protoconch conical, multispiral of three diagonally cancellate whorls. Length: 6.5 mm; breadth: 3 mm (figured syntype).

Remarks: *Taranidaphne nereidum* is readily distinguished from its congeners by its keeled whorls, pagediform spire, and absence of a strongly developed fenestrate sculpture. From *Taranidaphne hongkongensis* and *T. amphitrites* it further differs in its multispiral protoconch.

Although Melvill (1917) considered it very similar in ornamentation and shape to the Australian species *Daphnella vestalis* Hedley, 1903, the latter is rather different and has been referred to genus *Asperdaphne* (Laseron, 1954; Powell, 1966).

***Taranidaphne hongkongensis* (Sowerby, 1888),
comb.nov.**

(Figures 14–16)

Pleurotoma (Bela) hongkongensis Sowerby, 1888: 567, pl. 28, fig. 16. Type locality: Hong Kong
Bela erythraea Jousseaume, 1895:47. (new synonymy).
 Type locality: Atacka, Suez, Red Sea.
Taranis erythraeus (Jousseaume), Kilburn, 1991: 338, figs. 20–21.

Material examined: Two syntypes of *Pleurotoma (Bela) hongkongensis* stored in BMNH (reg. no 1889.2.1.9-10); lectotype and 10 paralectotypes of *Bela erythraea* in MNHN.

Remarks: Having examined the two syntypes of *P. (Bela) hongkongensis* and the type material of *Bela erythraea* Jousseaume, 1895, we consider these two to be synonyms. The two probably juvenile specimens of *P. (Bela) hongkongensis* (5.2 × 2.9 mm; 4.6 × 2.3 mm) agree remarkably well with the type series of *B. erythraea*, but superficially differ in having a slightly broader, globose protoconch (0.43–0.47 mm vs. 0.41 mm), fewer spiral lirae on the base (11–12 versus 12–15), and a strongly developed, nodulous subsutural ridge. Actually, these differences do not stand up to close scrutiny. In the largest specimen of *T. hongkongensis* the base is clearly damaged, so that the observed number of lirae (11) is only indicative. Furthermore, even within the type series of *Bela erythraea* there are considerable individual differences in the strength of the subsutural ridge, so that too much attention should certainly not be paid to this

character. We also assume that the very slight difference in protoconch breadth alone is rather inadequate to warrant a taxonomic distinction, even at the subspecific level.

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A New Genus and Species of Late Cretaceous Xenophorid Gastropod from Southern Mexico

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Abstract. A new genus and species of xenophorid gastropod, *Acanthoxenophora sinuosa*, is based upon well preserved specimens from the upper Maastrichtian deposits of the Mexcala Formation in Guerrero State, Mexico. The presence of attachment scars from foreign objects on the first three whorls and clusters of spines on the last whorls of the teleoconch distinguish this taxon from all other Late Cretaceous xenophorids. This occurrence represents the southernmost report of Maastrichtian xenophorids in North America.

INTRODUCTION

The discovery of several specimens of an unusual Late Cretaceous xenophorid gastropod from a region in which they were previously unknown provides the basis for definition of a new genus and species. This species documents an important geographic range extension for Late Cretaceous xenophorids, as will be discussed later. The specimens described in this work were collected from the Mexcala Formation at locality IGM 2490, north of Temalac, 125 km south of Mexico City and 70 km southeast of Iguala (Figures 1, 2).

The Mexcala Formation is a terrigenous sequence, the main outcrops of which are found in the state of Guerrero, southern Mexico. The formation ranges in age from Turonian in the central portion of Guerrero (Bohnenberg-Thomas, 1955; Böse, 1923; Dávila-Alcocer, 1974; González-Arreola, 1977; López-Ramos, 1983; Perrilliat, 1974; de Cserna et al., 1980; Ortega-Gutiérrez, 1980) to Maastrichtian in the study area in the northeastern portion of Guerrero (Alencáster, 1980; de Cserna et al., 1980; Ortega-Gutiérrez, 1980). This formation is part of a 3250 m-thick sedimentary sequence.

Previous paleontological reports for the area have described a few species of foraminiferans and mega-invertebrates, which are mostly ammonites. Alencáster (1980) first reported a diverse, yet poorly known, well preserved molluscan fauna from a single locality in Temalac. She illustrated 15 gastropod species without description. We have studied the area since 1990, making intensive collections at several localities north of Temalac. The fauna is now known to include planktic and benthic foraminifera; solitary, shallow-water hermatypic corals; gastropods; bivalves; scaphopods; reworked ammonoids and nautiloids; crabs; spatangoid echinoids; marine vertebrate remains; and palynomorphs. Previous paleontologic work on this fauna includes a species of retroplumid crab (Vega & Feldmann, 1992), as well as preliminary reports on the mollusks (Salceda et al., 1995; Vega & Perrilliat, 1995;

Perrilliat & Vega, 1996); and echinoids (Sánchez-Rodríguez et al., 1995; Sánchez-Rodríguez, 1997). The assemblage of invertebrate fauna is interpreted as shallow marine, possibly associated with a deltaic system. However, the abundance of planktic foraminifera and the broken delicate structures of the gastropod shells (aperture and spines), suggest that the material was reworked into a deeper environment, contemporaneously with the deposition of the planktic foraminifera.

An upper Maastrichtian age for the beds that contain the specimens here described was inferred based upon the presence of the following index species of foraminifera: *Gansserina gansseri* (Bolli), *Rosita fornicata* (Plummer), *Globotruncana ventricosa* (White), *G. linneiana* (d'Orbigny), *Rugoglobigerina rugosa* (Plummer), *Hedbergella monmouthensis* (Olsson), and *Heterohelix globulosa* (Ehrenberg). These species were identified by Brian Huber (personal communication). Several gastropod species have been described from the Maastrichtian of the Atlantic and Gulf Coastal Plains (Perrilliat et al., in press). Paleobiogeographic affinities of the late Maastrichtian molluscan fauna from Guerrero have shown the assemblage to be most closely related to the Atlantic and Gulf Coastal Plain Provinces (Perrilliat et al., in press).

Abbreviations used for catalog and locality numbers are: IGM, Instituto de Geología, Universidad Nacional Autónoma de México. Abbreviations used for measurements are: height = H; maximum diameter = D.

SYSTEMATIC PALEONTOLOGY

Superfamily XENOPHOROIDEA Troschel, 1852

Family XENOPHORIDAE Troschel, 1852

Genus *Acanthoxenophora* Perrilliat & Vega, gen. nov.

Type species: *Acanthoxenophora sinuosa* Perrilliat & Vega, from Temalac, Guerrero, late Maastrichtian.

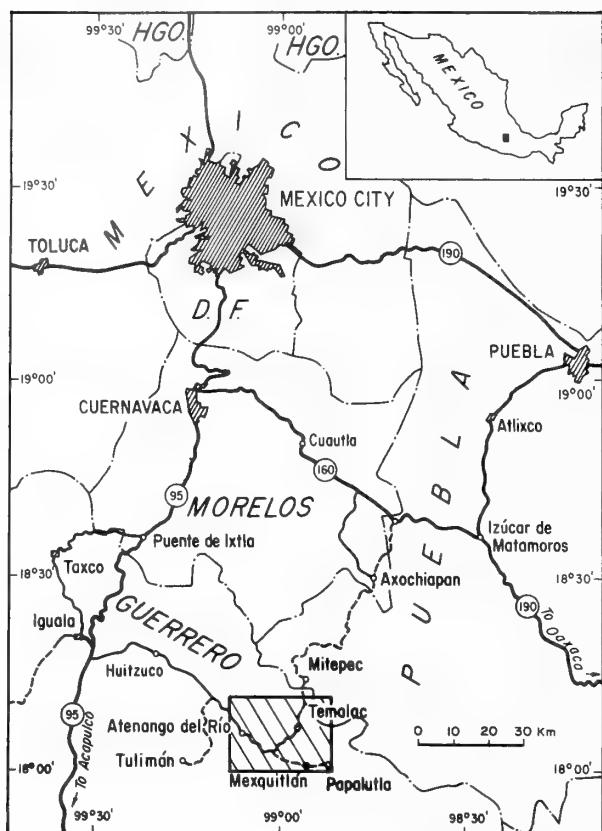


Figure 1. Location map of study area south of Mexico City. Framed area is enlarged in Figure 2.

Diagnosis: Shell small, conical. Low conical protoconch of three and a half whorls. From fourth to seventh whorl, ornamentation consists of long, paired sharp spines which appear at frequency of four per whorl. Non umbilicate.

Remarks: The resemblance of *Acanthoxenophora* in the typical xenophorid depressed-conical protoconch, smooth multispiral whorls, and the first whorls of the teleoconch with attached foreign objects suggests inclusion of *Acanthoxenophora* in the Xenophoridae. *Acanthoxenophora* lacks an umbilicus; the spinose sculpture on the fourth and later whorls of the teleoconch is a feature not present in any Xenophoridae, however.

Etymology: The generic name is compounded of *Acantho* derived from the latin root acanthus, meaning spine, and *Xenophora* meaning the presence of attached foreign objects in the first whorls as in the genus *Xenophora*.

Acanthoxenophora sinuosa Perrilliat & Vega,
sp. nov.

(Figures 3–13)

Diagnosis: As for genus.

Description: The shell is small, conical, higher than

wide, with seven whorls. The protoconch is conical, with three and a half whorls, and smooth. The first two to three whorls of the teleoconch with scars of foreign objects attached without any other ornamentation. On fourth and subsequent whorls there is a change in ornamentation, consisting of tubular spines and growth lines between spines. At the beginning of the fourth whorl three spines are present, one in the lower suture, and the other two above this spine, then every 15 degrees another set of three spines appears. Each spine is joined by thick lines of growth. The base of shell is slightly concave. Non umbilicate.

Holotype: IGM 4137

Paratypes: IGM 4138–IGM 4150 from IGM loc. 2940, Temalac, Guerrero, Mexico. Measurements (mm) of *Acanthoxenophora sinuosa* sp. nov.

	H	D
IGM 4137	20.0	17.4
IGM 4138	4.4	5.3
IGM 4139	14.6	13.5
IGM 4140	15.9	14.8
IGM 4141	3.6	3.5
IGM 4142	16.0	16.6

Geologic age: Late Maastrichtian.

Distribution: Mexcala Formation.

Discussion: There is no living or fossil genus characterized by ornamentation similar to the new genus here described.

Recent species *Xenophora (Stellaris) solaris* (Linnaeus, 1764) has a large shell with a peripheral flange with 10–20 long, narrow, tubular blunt spines. The inner peripheral flange has a narrow, weakly scalloped ridge from which spines arise at right angles to its periphery. These spines, however, are very different from the ones of the new genus.

The Jurassic genera *Jurassiphorus* Cossmann, 1915, and *Lamelliphorus* Cossmann, 1915, have often been discussed as the earliest xenophorids (Cossmann, 1915; Wenz, 1938; Ponder, 1983) although they do not show evidence of agglutinated particles.

The earliest typical *Xenophora*, according to Ponder (1983), is *Xenophora?* sp. (Stephenson, 1952:152) from the Cenomanian of Texas.

The Mexican specimens have no similarities to any species that have been described in the Upper Cretaceous. *Xenophora simpsoni* Stanton (1893:133, pl. 29, figs. 4–6) from the Turonian of Colorado (Figure 14), has a surface marked with depressions and holes caused by the adherence of small pebbles.

From the Neocomian of calcaire ferrugineux de Gy-l'Eveque, Peron (1900:74, pl. 3, fig. 2, 2, 2) described

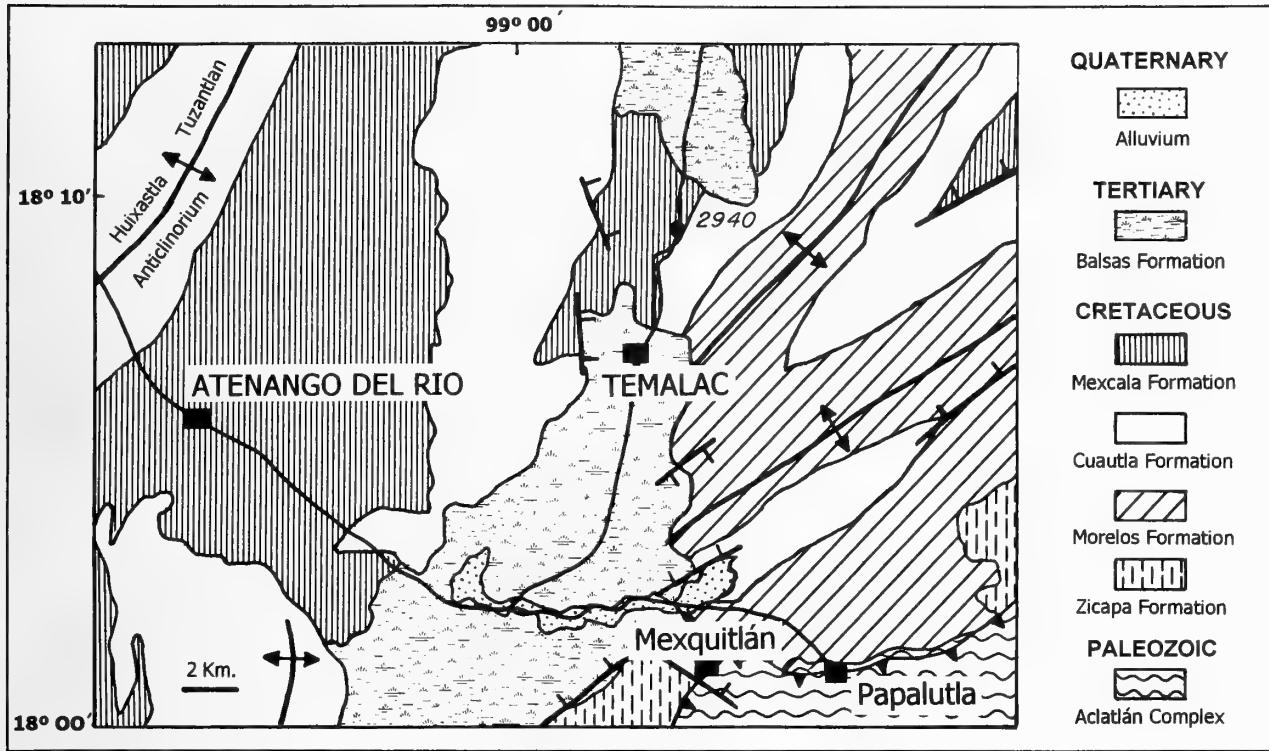


Figure 2. Location map showing locality IGM 2940.

Onustus tortilis characterized by 14 or 15 oblique ribs. These ribs form in the extremity a spinose point that surpasses the border of the shell; spiral striae are also present. The base is flat, smooth, and only presents spirals similar to the shell. Umbilicus is not present.

From the Senonian there are two known species: *Xenophora (Xenophora) canaliculatus* (d'Orbigny) (1842: 180, pl. 176, figs. 13, 14) from des couches supérieures de la craie, a Royan (Charente Inférieure) which has a conical shell, umbilicus not present; and *Xenophora umbilicatus* Tuomey (1854:169) from Noxubie County, Mississippi, which has a depressed shell with four whorls, concave below, suture deep umbilicus deep bordered by a channel. This could be *Xenophora leprosa* Morton.

From the Maastrichtian of Lemberg, Kner (1850:17, pl. 3, fig. 10) described *Xenophora (Xenophora) insignis*, and from Alabama a widely distributed species in the Gulf Coastal Plains, *Xenophora (Xenophora) leprosa* Morton (1834:46, pl. 15, fig. 6).

Xenophora (Xenophora) madagascariensis Collignon (1951:103, pl. 16, figs. 6, 6a, b) from Antonibe, Madagascar, a small species, conic, with flat whorls with agglutinated foreign bodies that later disappear. The base is flat with an umbilicus or rounded border, and no ornamentation. It is distinguished by its sharp carina and total absence of ornamentation. *Xenophora (Xenophora) onustus* Nilsson (1827:12, pl. 3, figs. 4A, B) from Sweden,

a species with four or five whorls, and in the whorls, the characteristic scars left by foreign objects.

From the Campanian of Southern India, Stoliczka (1868:247, pl. 19, fig. 24) described *Xenophora (Xenophora) carnatica*, with a small, broadly conical shell, composed of about seven flattened and regularly increasing volutions, the anterior edge of which is sharpened, and more or less irregularly interrupted by the impressions of foreign objects, which are attached to it.

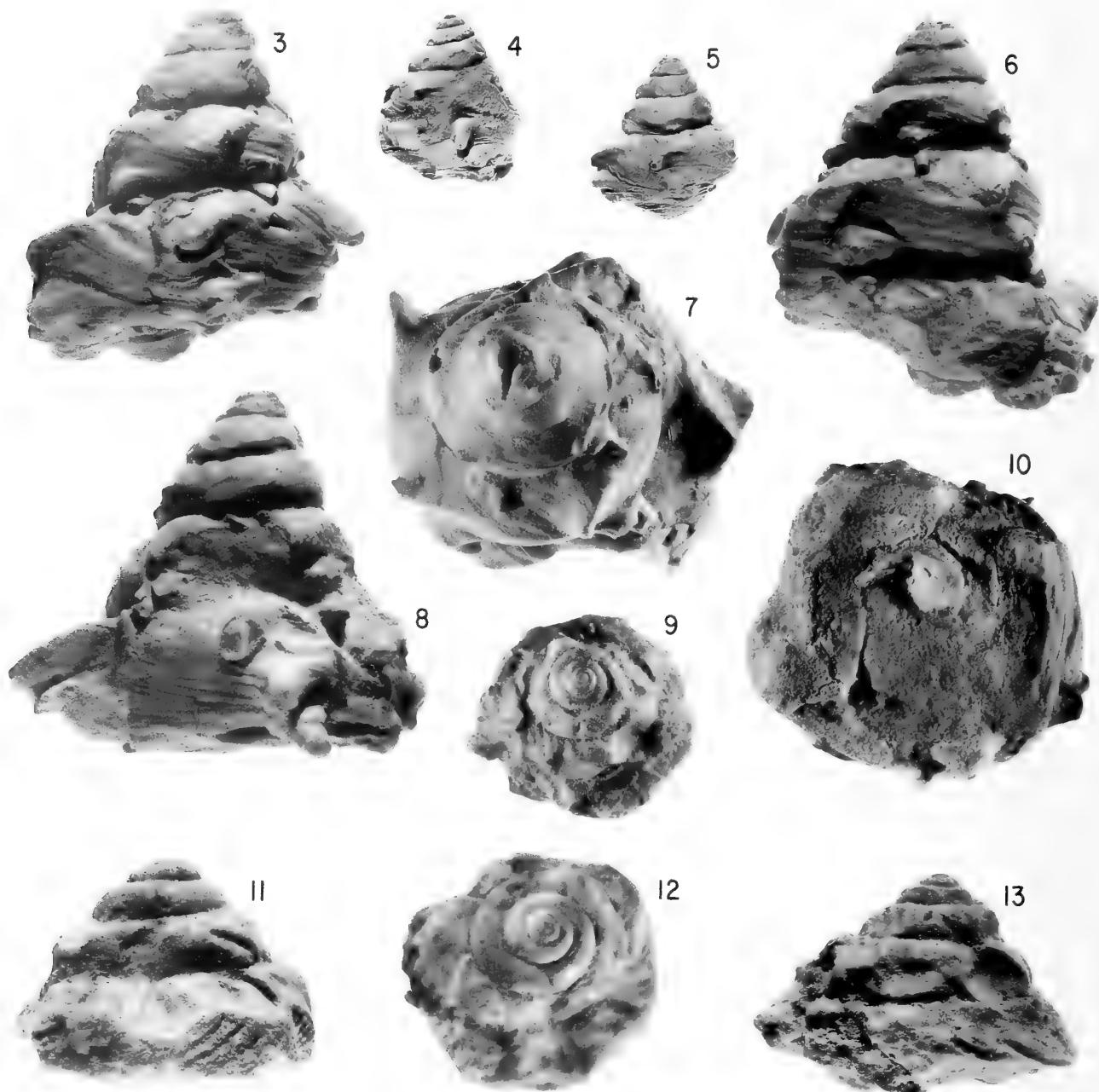
From the Santonian-Campanian of Masiadolo, Delpay (1948:23, pl. 5, fig. 1) described *Xenophora (Xenophora) coelatus*, a species with an ornamentation of oblique ribs from left to right; in the last whorl the superior ramp becomes spinose, and the growth lamellae form an almost longitudinal bundle that ends in spines.

Xenophora (Xenophora) plicatus (Zekeli) (1852:62, pl. 11, figs. 5a, b) from the Upper Cretaceous of Austria has in the first whorls foreign objects attached, but does not have spines.

From the late Campanian-early Maastrichtian of Baja California, Mexico, Webster (1983:1092, figs. 2A-F, 3A) described *Xenophora willisi*, particularly noteworthy for its large size, no fine superficial ornamentation preserved, broad base, concave, umbilicus completely closed.

None of these species bears spines as sculpture.

Etymology: The specific name *sinuosa*, refers to the sinuous shape of growth lines between spines.



Figures 3–13. *Acanthoxenophora sinuosa* Perrilliat & Vega, gen. & sp. nov. Figures 3, 6, 7. Holotype IGM 4137 from IGM loc. 2940. Figure 3. Back view; Figure 6. Aperture. Figure 7. Apical view, $\times 3$. Figure 4. Paratype IGM 4139 from IGM loc. 2940, back view, $\times 1.8$. Figure 5. Paratype IGM 4140 from IGM loc. 2940, back view, $\times 1.6$. Figure 8. Paratype IGM 4142 from IGM loc. 2940, back view, $\times 3.6$. Figures 9, 13. Paratype IGM 4138 from IGM loc. 2940. Figure 9. Apical view, $\times 6.9$. Figure 13. Back view, $\times 8.2$. Figure 10. Paratype IGM 4145 from loc. IGM 2940, basal view, $\times 5.2$. Figures 11, 12. Paratype IGM 4141 from IGM loc. 2940. Figure 11. Back view, $\times 10$. Figure 12. Apical view, $\times 10$. Photographs by A. Altamira.

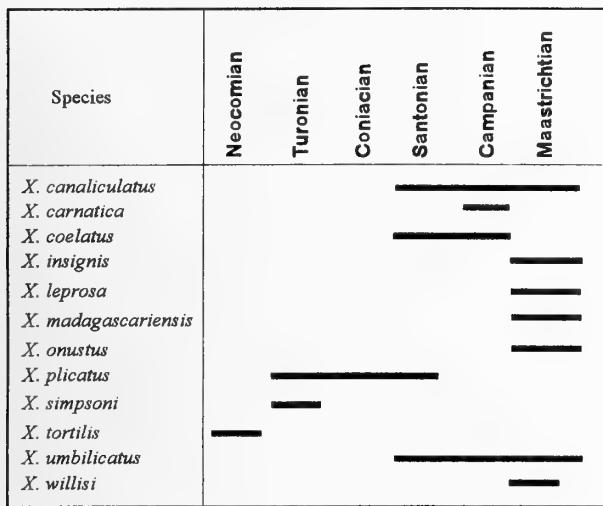


Figure 14. Stratigraphic range of the *Xenophora* species reported here.

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Chromosomal Location of the Major Ribosomal RNA Genes in *Crassostrea virginica* and *Crassostrea gigas*

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Abstract. The chromosomal location of the major ribosomal RNA genes (rDNA) was studied in the eastern oyster *Crassostrea virginica* (Gmelin, 1791), and the Pacific oyster *C. gigas* (Thunberg, 1793) by fluorescence in situ hybridization (FISH). Probes were made by PCR amplification of the intergenic transcribed spacers between the 18S and 5.8S (ITS1), and between 5.8S and 28S RNA genes (ITS2), and labeled by PCR incorporation of DIG-11-dUTP. FISH with either probe on interphase nuclei showed two strong signals in both species. In *C. virginica*, FISH signals were located on the short arms of Chromosome 2, the second longest, with a centromere index of 0.39. In *C. gigas*, the rDNA probe hybridized to the long arms of Chromosome 10, the shortest chromosome. In both species, the FISH signals were confined to the telomere region of the chromosomes. All *Crassostrea* species have a haploid number of 10, and *C. virginica* and *C. gigas* share an almost indistinguishable karyotype. The size of the rDNA-bearing chromosome is the first major difference reported between the two karyotypes. This result suggests that considerable chromosomal evolution is possible in oysters despite the highly conserved haploid number.

INTRODUCTION

Oysters are important species for aquaculture, supporting major industries worldwide. The need for genetic analysis and improvement in oysters is great. At present, we know little about the genome of oysters including its most basic units—chromosomes. Chromosome characterization and identification remain difficult in oysters and most other marine mollusks. Chromosome identification is necessary for studies on aneuploids, chromosomal assignment of genes, and the development of chromosome-specific libraries and markers. Trisomic families have been produced in the Pacific oyster, *Crassostrea gigas* (Thunberg, 1793) (Guo et al., 1998); and their identification and analysis have been difficult.

Oysters appear to have highly conserved karyotypes. All species of *Crassostrea* studied so far have a haploid number of 10 chromosomes (Nakamura, 1985). Although the haploid number is low, oyster chromosomes are small and similar in size and arm ratio, and do not permit tra-

ditional banding analyses. One banding study has been reported in the eastern oyster *C. virginica* (Gmelin, 1791) with limited resolution (Rodriguez-Romero et al., 1979). C- and G-banding patterns have been produced in *C. gigas*, but the reproducibility is low (Guo et al., unpublished). Recently, fluorescence in situ hybridization (FISH) has been used to characterize oyster chromosomes. A satellite DNA sequence has been assigned to two chromosomes of *C. gigas* (Clabby et al., 1996). The vertebrate telomere sequence, (TTAGGG)_n, has been localized to telomeres of *C. gigas* (Guo & Allen, 1997).

As part of our effort to characterize oyster chromosomes, we studied the location of major ribosomal RNA genes (or rDNA) in *C. virginica* and *C. gigas* with FISH. The major rDNAs in animals are present in tandem repeats of hundreds to thousands of units, and each unit contains the 18S, 5.8S, and 28S genes and intergenic spacers (Lewin, 1994). Ribosomal DNA has been assigned to specific chromosomes with FISH in many plants and animal species (De La Rúa et al., 1996). In some oysters, the location of rDNA has been studied indirectly by silver-staining of the nucleolar organizer re-

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gions (NORs), and intraspecific variation in the number and size of NORs has been observed (Thiriot-Quiévreux & Insua, 1992; Li & Havenhand, 1997). Intraspecific variation in NORs is common in fish and marine bivalves (Gold, 1984; Thiriot-Quiévreux & Insua, 1992). This variation may be caused by artifacts or differences in gene expression and/or DNA sequence, and FISH analysis with rDNA probes should be helpful. Here we report, for the first time, the localization by FISH of major rDNA on chromosomes of two species of *Crassostrea*.

MATERIALS AND METHODS

The *C. virginica* used for this study were from the Rutgers NEH strain. This strain has been selectively bred for over 36 years, primarily for disease-resistance. The *C. giga* used were from a stock that was originally introduced from Washington State and has been maintained in a quarantine system at Rutgers for five generations. Metaphase chromosomes were obtained from early embryos as described by Guo et al. (1992). Briefly, eggs and sperm were collected from mature oysters by stripping gonads. Eggs were passed through a 70- μm nytex screen to remove large tissue debris, and rinsed on a 20-mm screen. Eggs were resuspended in seawater and fertilized by adding sperm suspension. Excessive sperm were removed at 15 min post-fertilization by rinsing fertilized eggs on a 20- μm screen. Embryos were resuspended and cultured at 25°C. After 5 to 6 hours of culture, embryos were harvested into a 15 ml tube and treated with 0.005% of colchicine for 30 min. Colchicine was removed by pelleting out embryos with centrifugation. Nine parts of 0.075 M KCl were added to every part of concentrated embryos, and the hypotonic treatment lasted for 10 min. Embryos were then fixed in 1:3 acetic acid and methanol and stored at 4°C. For slide preparation, two to three drops of embryo suspension were loaded onto a slide and air-dried. Slides were stored at -20°C until FISH.

Intergenic transcribed spacers between the 18S and 5.8S (ITS1), and between 5.8S and 28S RNA genes (ITS2) were amplified and labeled by PCR, and used as FISH probes. PCR primer sequences are 5'-GGTTTCTGTAGGT-GAACCTGC and 5'-CTGCGTTCTTCATCGACCC for ITS1, and 5'-GGGTCGATGAAGAACGCAG and 5'-GCTCTTCCCGCTTCACTCG for ITS2. Probes were labeled with digoxigenin-11-dUTP (alkali-stable) by PCR incorporation. Digoxigenin-11-dUTP and all other PCR reagents were purchased from Boehringer Mannhem (Indianapolis, Indiana). PCR reactions were performed in 25 μl volume containing 1 \times PCR buffer with 1.5 mM of MgCl₂, 0.4 mg/ml of BSA, 0.2 mM each of dATP, dCTP, and dGTP, 0.13 mM of dTTP, 0.07 mM of Digoxigenin-11-dUTP, 0.5 U of Taq DNA polymerase, 0.2 μM of each primer, and 1 μg of oyster genomic DNA. Thermal cycling parameters were 30 cycles of 1 min at 95°C, 1 min at 50°C, and 1 min at 72°C. The PCR product was purified

through a G-50 column to remove unincorporated nucleotides.

All FISH reagents were purchased from Oncor, Incorporated. (Gaithersburg, Maryland). FISH was conducted according to the protocol recommended by Oncor and as described by Guo & Allen (1997). To prepare the probe for hybridization, 1.5 μL of the purified PCR product was added to 30 μL of Hybrisol VI (Oncor) and incubated at 72°C for 5 min. Slides carrying metaphase spreads were incubated in 2 \times SSC at 37°C for 30 min, dehydrated for 2 min each in 70%, 80%, and 95% EtOH, and air-dried. Slides were then denatured in 2 \times SSC containing 70% deionized formamide at 72°C for 2 min, dehydrated for 2 min each in cold 70%, 80%, and 95% EtOH, and air-dried. The denatured probe (30 μL) was added to the slides and covered with 22 \times 50 mm glass coverslips. After sealing with rubber cement, the slides were incubated at 37°C in a humidified chamber overnight. Coverslips were then removed, and slides were washed in 1 \times SSC at 72°C for 5 min and 1 \times PBD at room temperature for 2 min. Fluorescein-labeled anti-digoxigenin antibody (60 μL) was added to the slides, covered with plastic coverslips, and incubated at 37°C for 10 min in a humidified chamber. Slides were then washed three times for 2 min each in 1 \times PBD at room temperature in the dark. Propidium iodide/antifade (10 μL) was added to each slide and covered with glass coverslips. Hybridization signals were analyzed and documented using a 3CCD camera and the Image-Pro Plus image system. Centromeric index was calculated as the length of short arm divided by total length (Levan et al., 1964).

RESULTS

PCR amplification in *C. virginica* generated a single product with both primer sets, ITS-1 and ITS-2. In the absence of digoxigenin-11-dUTP, ITS-1 generated an approximately 500 bp product, and ITS-2 generated a 750 bp product (Figure 1, lanes 2 and 3). The incorporation of digoxigenin-11-dUTP significantly decreased the mobility of both products, with the ITS-1 product shifted to 650 bp and the ITS-2 product to 900 bp (Figure 1, lanes 4 and 5). Production of ITS-1 probe was more reliable probably because of the smaller fragment size than ITS-2. Cleaning of labeled probes with columns clearly reduced background signals from FISH.

The embryo material was adequate for FISH analysis. Early embryos with four to eight cells contained a large amount of yolk material, which gave high background signals. Most of the embryos used in this study were between 30 and 120 cells and actively dividing. Four to 10 good metaphases were often obtained per slide.

In situ hybridization with ITS-1 probe to interphase nucleus consistently produced two clusters of signals per nucleus in *C. virginica* (Figure 2A). FISH signals within a cluster appeared to be discontinuous or fragmented.

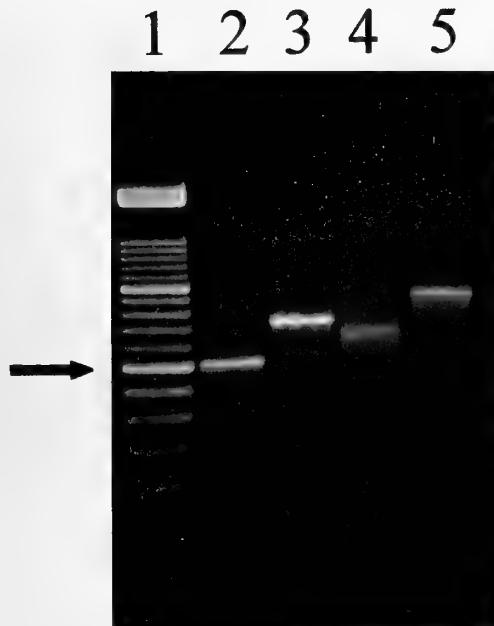


Figure 1. Products of PCR amplification of intergenic transcribed spacers between 18S and 5S (ITS1), and 5.8S and 28S RNA genes (ITS2), and the labeled fragments in *Crassostrea virginica*: Lane 1, 100 bp ladder; Lane 2, ITS1 product; Lane 3, ITS2 product; Lane 4, labeled ITS1; Lane 5, labeled ITS2.

FISH of ITS-1 on metaphase chromosomes showed that the signals were located on the telomeric region of the short arms of one pair of homologous chromosomes (Figure 2B). To characterize the hybridized pair of chromosomes, homologous chromosomes from six metaphases were paired, measured, and numbered as Chromosome 1 to 10 according to their length (Table 1). The FISH signals were clearly located on Chromosome 2 (Figure 2C,E), which was the second longest and had a centromeric index of 0.39. Chromosomes 1, 2, and 10 were clearly distinguishable from others because of their length and arm-ratio. The pairing of the other homologous chromosomes was less certain. FISH with the ITS-2 probe produced exactly the same pattern of signals that was indistinguishable as with ITS-1 (data not shown).

PCR amplification of ITS-1 in *C. gigas* produced a single fragment which is slightly longer than that from *C. virginica*. FISH with ITS-1 on *C. gigas* nuclei showed two clusters of signal per nucleus. Analysis of FISH signals on metaphase chromosomes revealed that signals are located in the telomeric region of the long arms of Chromosome 10, the smallest chromosomes (Figure 2D, E). FISH with ITS-2 produced the same results (data not shown). The FISH signal was often stronger in one of the homologous chromosomes, and the differential intensity was noticeable even when the two homologous chromosomes were closely situated in the metaphase (Figure 2D).

Table 1

Karyotype analysis of *Crassostrea virginica* chromosomes.

Chromosome number	Length as percent total length of haploid complement (\pm SD)	Centromeric Index ¹ (\pm SD)
1	12.30 \pm 0.23	0.48 \pm 0.02
2	11.41 \pm 0.09	0.39 \pm 0.01
3	10.80 \pm 0.09	0.42 \pm 0.01
4	10.71 \pm 0.12	0.48 \pm 0.01
5	10.45 \pm 0.11	0.41 \pm 0.01
6	9.99 \pm 0.19	0.41 \pm 0.01
7	9.54 \pm 0.22	0.38 \pm 0.04
8	8.73 \pm 0.24	0.48 \pm 0.01
9	8.65 \pm 0.14	0.36 \pm 0.05
10	7.42 \pm 0.14	0.48 \pm 0.02

¹ Length of short arm divided by total length (Levan et al., 1964).

DISCUSSION

The major rDNA genes (18S, 5.8S, and 28S) are unambiguously assigned to chromosomes of *C. virginica* and *C. gigas*. This study provides the first chromosomal assignment of genes with FISH in oysters and possibly all marine mollusks. Protocols for chromosome preparation, probe labeling, and FISH used in this study are highly reproducible for oysters and should promote FISH analysis in other marine mollusks. Mollusks represent a major taxon for evolutionary studies, and information about molluscan genomes is important for comparative genomics.

Results of this study clearly show that there is only one site for the major rDNA cluster (18S, 5.8S, and 28S) in the two species, which confirms the previous observation of one pair of NOR-chromosomes in *C. gigas* (Thiriot-Quiévreux & Insua, 1992). No comparable data from *C. virginica* and other *Crassostrea* species are available. Two or more NOR-chromosomes have been observed in several *Ostrea* oyster species (Insua & Thiriot-Quiévreux, 1991, 1993; Thiriot-Quiévreux & Insua, 1992; Li & Hayenhand, 1997) and three *Mytilus* mussel species (Insua et al., 1994).

Intraspecific variation in the number and size of NORs is common in fish and marine bivalves (Gold, 1984; Thiriot-Quiévreux & Insua, 1992). This variation may be caused by artifacts, differences in gene expression or DNA sequence, and has rarely been confirmed with FISH analysis. In *C. gigas*, no variation in the number of NOR-chromosomes has been observed, but the two homologous chromosomes differ in the size (or intensity) of NORs (Thiriot-Quiévreux & Insua, 1992). We also noticed that the FISH signals are often considerably stronger on one of the homologous chromosomes than the other

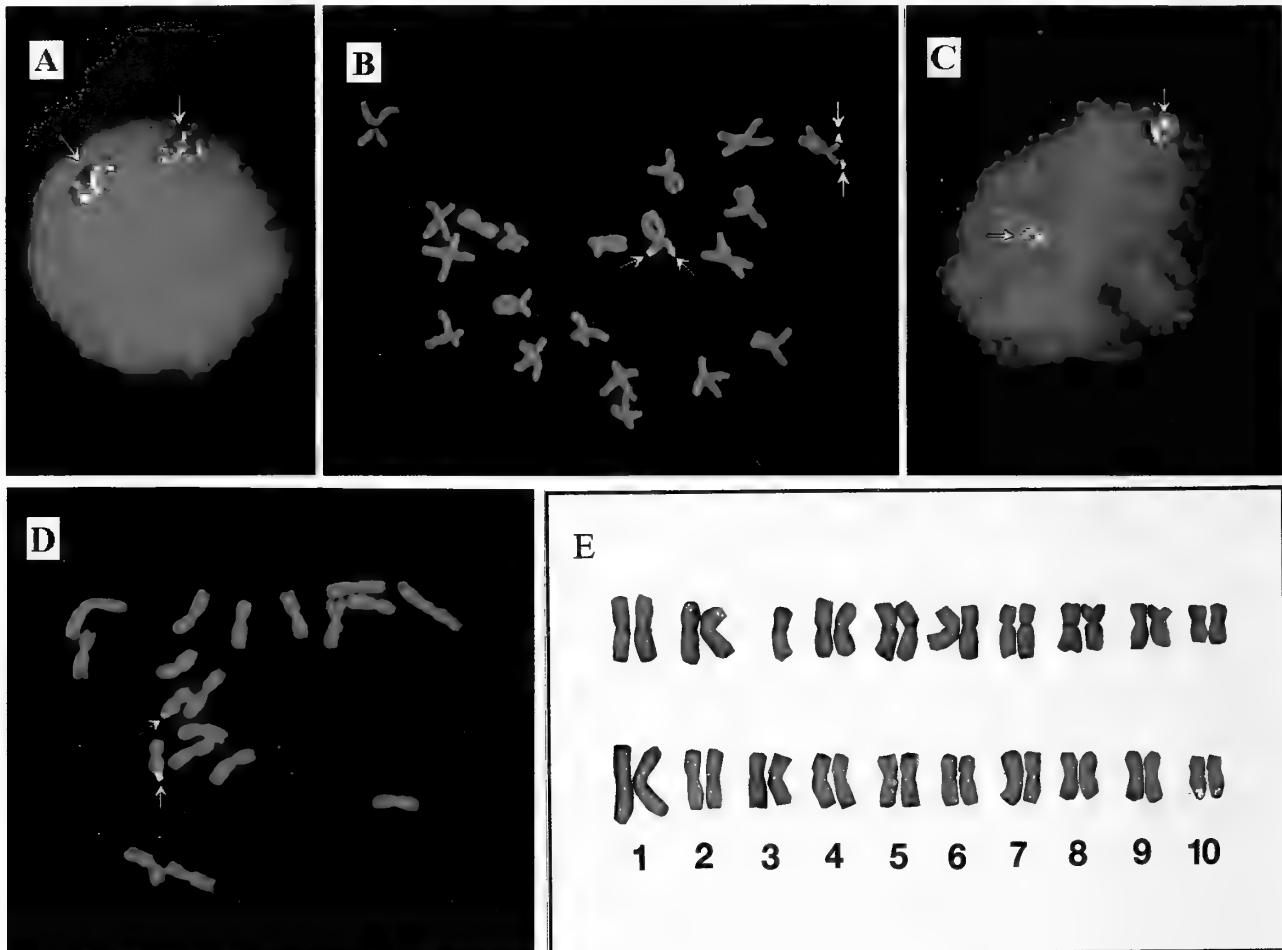


Figure 2. FISH with the rDNA probe (ITS1) on interphase nuclei and metaphase chromosomes in *Crassostrea virginica* and *C. gigas*. A. *C. virginica* nucleus; B. *C. virginica* metaphase; C. *C. gigas* nucleus; D. *C. gigas* metaphase; and E. karyotypes of *C. virginica* (upper) and *C. gigas* (lower), with rDNA probe hybridized to Chromosomes 2 and 10, respectively. Arrows indicate FISH signals.

(Figure 2D). The same is true with telomeric repeats in *C. gigas* (Guo & Allen, 1997). The differential intensity may be superficial and caused by random variation in FISH, or it may reflect true differences (loss or gain) in DNA sequence. Also, FISH signals in interphase nuclei were fragmented, which may suggest that there is significant space among the repetitive units or clusters of units. This phenomenon has also been observed in tiger beetles (De La Rúa et al., 1996).

Interspecific variation in rDNA or NOR location is expected and has been used for phylogenetic analysis (De La Rúa et al., 1996). Ribosomal DNA is found in telomeric regions of chromosomes in both oysters. In *C. virginica*, analysis of multiple karyotypes positively assigns the rDNA on the short arm of Chromosome 2, the second longest chromosome. Our karyotype for *C. virginica* closely resembles a previously described one in the same species, except that Chromosome 2 was named Chromosome 3 in the previous study, according to centromeric

index, rather than total length (Longwell et al., 1967). In *C. gigas*, the rDNA is clearly located at the long arm of Chromosome 10, the smallest chromosomes, confirming results from NOR analysis (Thiriot-Quiévreux & Insua, 1992). The karyotypes of the two species are almost indistinguishable, and the difference in the rDNA-bearing chromosome is the first major difference between the two karyotypes recognized to date. This observation suggests that considerable chromosomal evolution is possible in oysters despite the highly conserved haploid number.

The rDNA FISH probe provides an effective method for the identification of Chromosomes 2 and 10 of *C. virginica* and *C. gigas*, respectively. We are in the process of developing additional chromosome-specific FISH probes for trisomic analysis in oysters (Guo et al., 1998).

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Conchocele bisecta (Conrad, 1849) (Bivalvia: Thyasiridae) from Cold-Water Methane-Rich Areas of the Sea of Okhotsk

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Abstract. Dense aggregations of *Conchocele* sp., containing sulfur- and methane-oxidizing endosymbiotic bacteria, were found in 1986 near cold-water methane-rich seeps off Paramushir Island (Kuril Islands, Sea of Okhotsk, depth 750–804 m). Upon examination of shell morphology and gross anatomy, this species proved to be *Conchocele bisecta* (Conrad, 1849) widely distributed in the northern Pacific Ocean. This is the first record of this species in Russia. In the Sea of Okhotsk it is found only in zones of cold-water methane-rich seeps. We presume that *C. bisecta* also occurs in other parts of its range in organic-rich sediments with high total methane and sulfide concentrations. A description of *C. bisecta*, including some additional data on shell morphology, gross anatomy, geographic distribution, and habitat, is presented.

INTRODUCTION

In the spring of 1982, fishermen and then researchers of the Institute of Volcanology, Russian Academy of Sciences, found sound-scattering anomalies northwest of Paramushir Island, Kuril Islands ($50^{\circ}30.8'N$, $155^{\circ}18.45'E$) (Avdeiko et al., 1984; Obzhirov, 1993). The studies of volcanologists have shown that the anomalies were formed by gas plumes of methane-rich fluids from a gas hydrate area on the submarine slope of Paramushir Island (depth 750–800 m). In June–July 1986, a joint expedition of the Institute of Oceanology, Russian Academy of Science (R/V *Akademik Mstislav Keldysh*) and the Institute of Volcanology (R/V *Vulkanolog*) examined these methane-rich vents and the benthic animals (Kuznetsov et al., 1987, 1989). Dense aggregations of the bivalve *Conchocele* sp. and a polychaete of the family Ampharetidae were found immediately near the vents. The polychaete was subsequently assigned to a new genus and described as *Pavelius ushakovi* Kuznetsov & Levenstein, 1988 (Kuznetsov & Levenstein, 1988). The bivalves were large (shell length 12 to 15 cm [Kuznetsov et al., 1991]) and had some anatomical features suggesting that they were a new species (Kuznetsov et al., 1987, 1989). Study revealed the presence of sulfur- and methane-oxidizing symbiotic bacteria in the body of *Conchocele* sp. (Galchenko et al., 1988a, b; Strizhov et al., 1990; Kuznetsov et al., 1991). Bacterial symbiotrophy proved to be the principal mode of feeding

by *Conchocele* sp. near methane-rich vents of Paramushir Island, supplemented by sestonophagy. However, despite all these investigations, the morphological study of the shell and the identification of this species have not yet been performed.

Expeditions of 1996–1998 of the Pacific Research Institute of Fisheries and Oceanography (R/V *Professor Kaganovsky*; R/V *TINRO*) in the Seas of Japan and Okhotsk found abundant fresh valves and live individuals of a species of the genus *Conchocele* Gabb, 1866. Moreover, in collections of the Zoological Institute, Russian Academy of Sciences, and the Pacific Research Institute of Fisheries and Oceanography, we found unrecorded material of this species from the Sea of Okhotsk and the Pacific Ocean. We were also given materials on *Conchocele* sp. from Paramushir Island deposited at the Institute of Oceanology, Russian Academy of Sciences. Comparative analysis of the results of research in shell morphology and the gross anatomy of these specimens with descriptions and pictures of all species of the genus *Conchocele* occurring in the northern Pacific showed that we are dealing with one species, the well known *Conchocele bisecta* (Conrad, 1849). This is the first record of this species for the Russian fauna.

Shell morphology and anatomy of the soft parts of Recent *C. bisecta* are described in several works (Oldroyd, 1924; Nakazima, 1958; Bernard, 1972; Kuznetsov et al.,

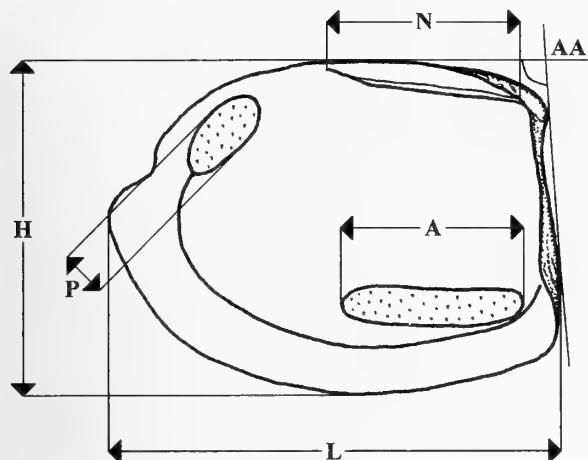


Figure 1. Placement of shell measurements: A—length of anterior adductor scar; AA—apical angle; H—height; L—shell length; N—length of nymph; P—width of posterior adductor scar.

1991). Nevertheless, the discovery of this species in different areas of the Seas of Okhotsk and Japan supplements the description of this species with new data on shell morphology, anatomy, and distribution in the northwestern Pacific.

The following abbreviations are used: IMB, Institute of Marine Biology, Russian Academy of Sciences, Vladivostok; MIMB, Museum of the Institute of Marine Biology, Vladivostok; IORAS, Institute of Oceanology, Russian Academy of Sciences, Moscow; PRIFO, Pacific Research Institute of Fisheries and Oceanography, Vladivostok; ZIN, Zoological Institute, Russian Academy of Sciences, S.-Petersburg; ZMU, Zoological Museum of Far East State University, Vladivostok.

MATERIALS AND METHODS

In this study we have used the material of *C. bisecta* collected by expeditions PRIFO (Kyushu-Palau Ridge, Pacific Ocean, R/V *Mys Tikhii*, 1982; Sea of Japan, R/V *Professor Kaganovsky*, 1996; west coast of Kamchatka, Sea of Okhotsk, R/V *TINRO*, 1997, 1998), IORAS (Paramushir Island, R/V *Akademik Mstislav Keldysh*, 1986; northeastern coast of Sakhalin Island, R/V *Akademik M.A. Lavrentiev* 1998), ZIN (southeastern coast of Sakhalin Island, R/V *Novoulyanovsk*, 1984; northeastern coast of Sakhalin Island, R/V *Novodrutsk*, 1987).

All live specimens from various collection areas were fixed in 4% formaldehyde solution and then with 70% ethanol.

Figure 1 shows the position of our shell morphology measurements. Shell length (L), height (H), width of each valve (W) (not shown on the picture), length of anterior adductor scar (A), width of posterior adductor scar (P), length of nymph (N) and apical angle (AA-angle between

the line parallel to the ventral nymph margin and the line parallel to the anterior shell margin or [if the anterior shell margin is concave] the line running through the beak and shell angle formed at the transition of the anterior into ventral shell margin) of intact and partially damaged specimens were measured, and ratios of some of these parameters to shell length (H/L, W/L, A/L, P/L, and N/L) were determined. Shell measurements were made using calipers with an accuracy of 0.1 mm.

The gross anatomy and internal structure has been described from whole mount specimens.

SYSTEMATICS

Conchocele bisecta (Conrad, 1849)

(Figures 2–22, Table 1)

Venus bisecta Conrad, 1849:724, pl. 17, figs. 10, 10a.
Conchocele disjuncta Gabb, 1866:27, pl. 7, fig. 48a, b.

Type material and locality: *Venus bisecta*, holotype (USNM 3518), two almost complete valves, length 46.5 mm (incomplete), height 53 mm (incomplete), thickness 38.9 mm (incomplete); paratypes (USNM 561518 (originally USNM 3518), 563440 (originally USNM 3500)), five specimens; Astoria, Oregon, Miocene fossil (Moore, 1963).

Conchocele disjuncta, lectotype (Academy of Natural Sciences, Philadelphia); Deadman Island, near San Pedro Bay, California, Pliocene fossil (Bernard, 1972).

Material examined: Three lots from the northeastern Sea of Okhotsk (57°02'N, 152°29'E–57°16.8'N, 152°40.4'E), 482–491 m, silty sand + H₂S, bottom temperature 1.65°C, Coll. V. A. Nadtochy, 14 October 1997 and I. V. Volvenko, 3 November 1998 (R/V *TINRO*) two whole specimens; ZMU (no number), one whole specimen and one right valve); one lot from west coast of Kamchatka, Sea of Okhotsk (55°00'2"N, 154°06'3"E), 522–531 m, mud + H₂S, bottom temperature 2.2°C, Coll. V. A. Nadtochy, 15 September 1997 (R/V *TINRO*) (one whole specimen, six right and four left valves); one lot from Paramushir Island, Kuril Islands, Sea of Okhotsk (50°30.88'N, 155°18.14'E), 792–804 m, mud + H₂S, Coll. A. P. Kuznetsov, 4 July 1986 (R/V *Akademik Mstislav Keldysh*) (IORAS (no number), one whole specimen and one right valve); two lots from northeastern coast of Sakhalin Island, Sea of Okhotsk (52°22'9"N, 144°38'4"E), 502–517 m, mud + H₂S, Coll. V. V. Fedorov, 28 July 1987 (R/V *Novodrutsk*) (ZIN (no number), one whole specimen) and (54°26.751'N, 144°04.940'E), 702 m, sandy silt + shell fragments, Coll. S. V. Galkin, 17 August 1998 (R/V *Akademik M. A. Lavrentyev*) (one whole specimen, one right valve); two lots from southeastern coast of Sakhalin Island, Sea of Okhotsk (45°53'2"N, 143°53'E and 47°14'8"N, 143°42'7"E), 510 m and 300–320 m, correspondingly, silty sand, Coll. S. D. Grebelny, 19 and 20

September 1984 (R/V *Novoulyanovsk*) (ZIN (no number), one left and one right valves); one lot from Sea of Japan (42°19.6'N, 131°10.6'E), 130 m, silty sand, Coll. V. V. Gulbin and Yu. M. Yakovlev, 20 May 1996 (R/V *Professor Kaganovsky*) (MIMB (no number), three right and one left valves; ZMU (XII 14973/Bv-1936), one right valve); one lot from Kyushu-Palau Ridge south of Shikoku Island (Japan), Pacific Ocean (24°46'N, 134°39'E–28°03'N, 135°39'E), 3–18 January 1982 (R/V *Mys Tikhii*) (PRIFO (no number), two right and two left valves). Total of seven whole specimens, 16 right and eight left valves.

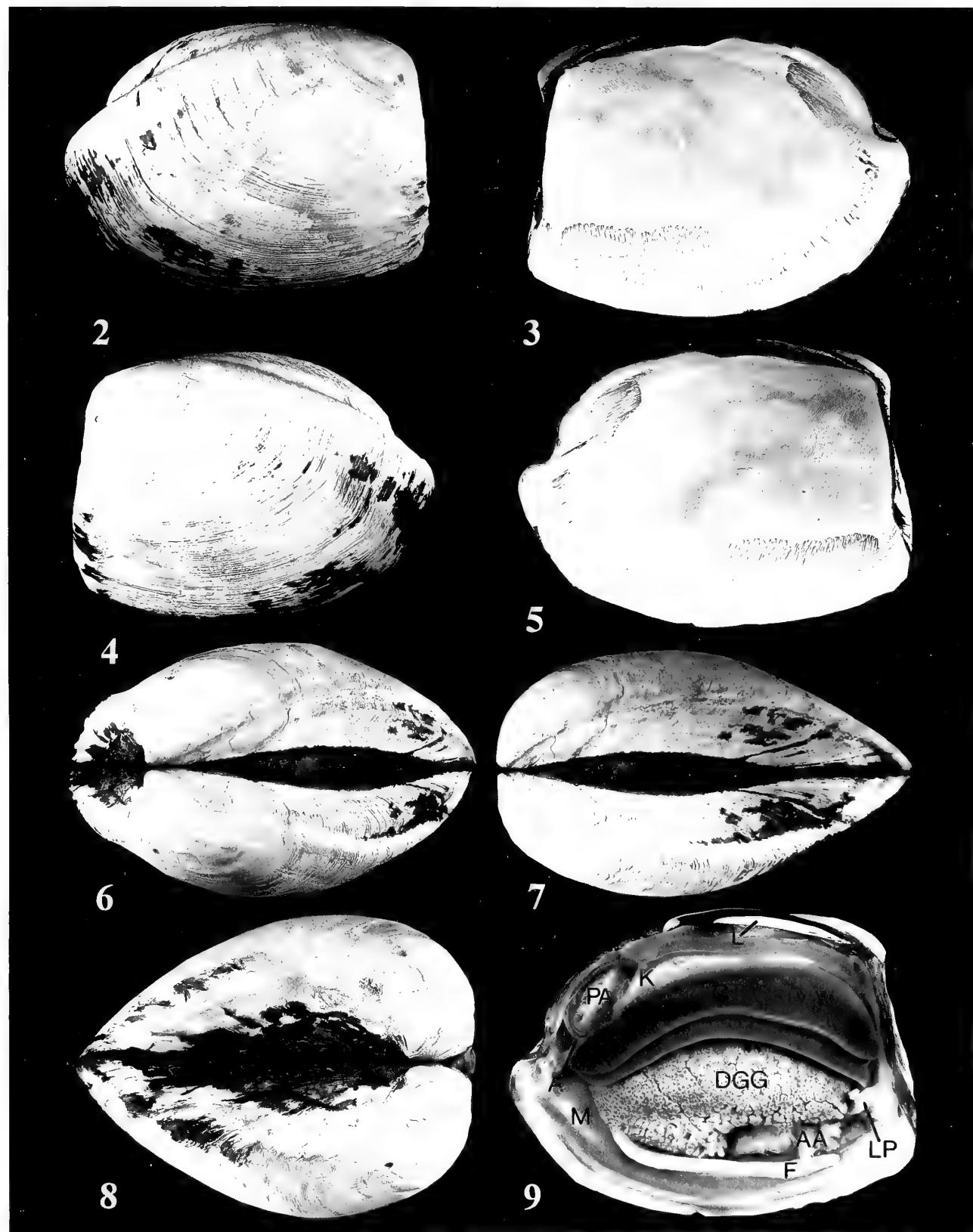
Description: Exterior: Shell very large (to 165.4 mm in length), thick, inequilateral, equivalve (left valve sometimes slightly more inflated), subquadrate, elongated posteriorly, apical angle 90°–125°, high ($H/L = 0.69$ –0.84), convex ($W/L = 0.22$ –0.33), white under periostracum. Periostracum thin, gray-yellow, not adherent, usually peeled off near beaks, in adult specimens preserved only on shell margins. Surface with conspicuous growth lines. Beaks small, prosogyrate, terminal, anteriorly placed. Anterior end abruptly truncated. Posterior end ovate-angulate with distinct radial sulcus extending from beaks to tip, forming deep notch in posterior shell margin and separating distinct posterodorsal depressed area from main part of valve; another very faint radial ridge extending from beaks to ventral shell margin causing hardly noticeable ventral angulation. Anterior shell margin straight (sometimes concave), almost vertically extending ventrally, forming distinct (almost right) angle at transition to ventral shell margin. Ventral shell margin slightly curved. Posterodorsal shell margin straight or slightly convex, extending almost horizontally, parallel to ventral margin, forming rounded angle at transition to posterior shell margin. Posterior shell margin rounded, with deep notch, smoothly transitioning to ventral margin. Lunule just below beaks, smooth, wide, well expressed along entire anterior shell margin, demarcated by the ridges extending along anterior shell margin from beaks to ventral shell margin. Escutcheon absent. Ligament opisthodetic, external, long and elliptical, with calcareous deposition in inner layer, partly sunken, extending from beaks to posterior pedal retractor muscles, attachment to strong and broad nymph, consisting of three layers: periostracum ligament layer, outer ligament layer, and inner ligament layer.

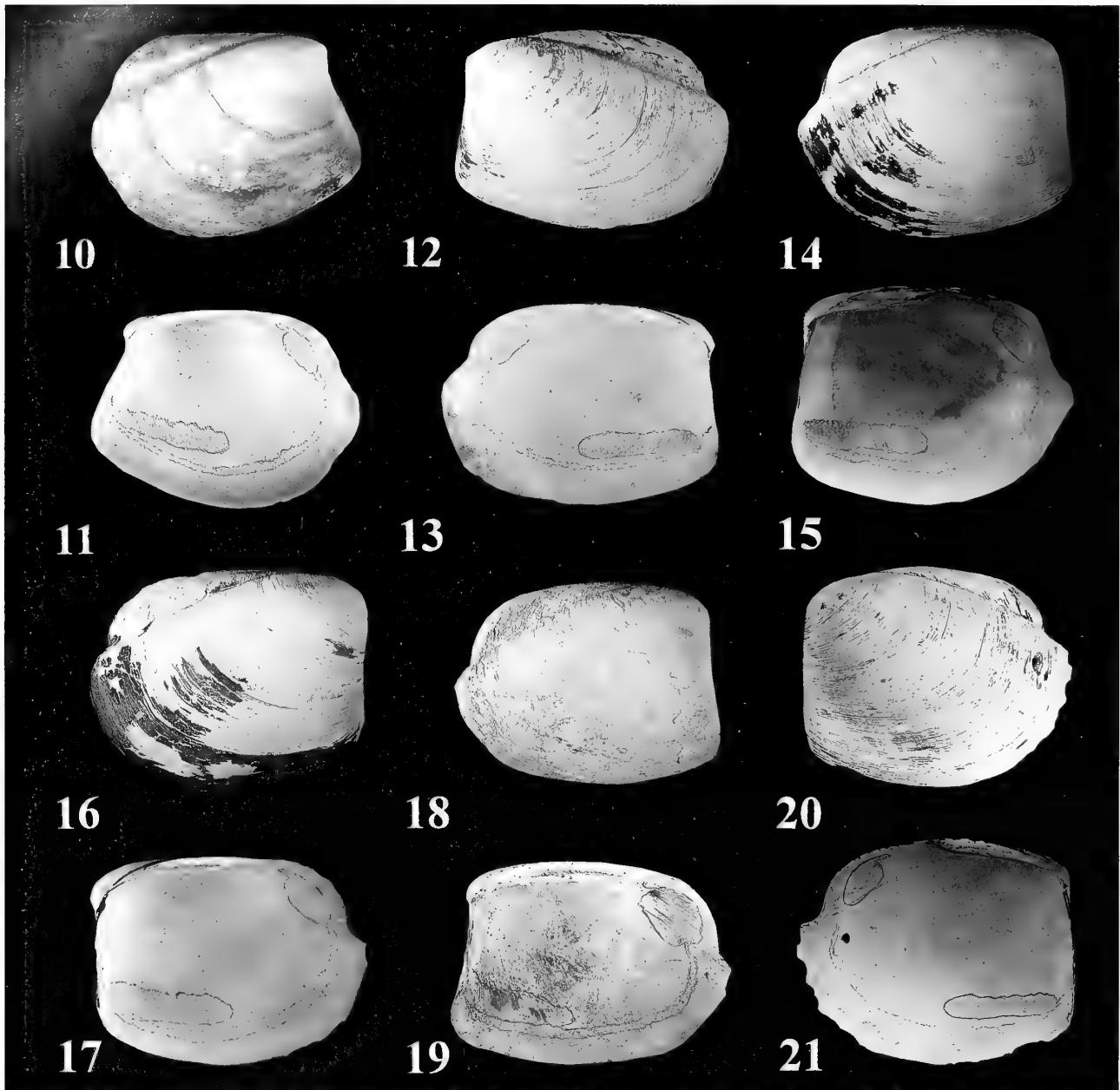
Interior. Hinge plate thin, without teeth. Nymph strong,

long ($N/L = 0.33$ –0.63), wide, with a small shelf along ventral nymph margin, extending from beaks to three-quarters of distance to posterior shell margin. Pallial line without pallial sinus. Anterior muscle scar large, long ($A/L = 0.40$ –0.48), ovately elongate, extending almost parallel to ventral shell margin. Posterior muscle scar small ($P/L = 0.12$ –0.21), ovate. Interior of valves white, smooth, with fine radiating striae, more visible near anterior muscle scar; sulci visible as two prominent ridges.

Gross anatomy: Mantle thin, margins thickened. Mantle fusion limited to a small interconnection below the posterior adductor, forming a posterior exhalant aperture. Anterior adductor muscle very large, greatly elongated, curved almost parallel to ventral shell margin. Posterior adductor muscle small, broader than anterior, ovate. Foot long, vermiform, with bulbous distal section. Anterior pair of narrow pedal retractor muscles passing as a single sheet of muscle from base of foot parallel to dorsal margin of posterior adductor toward either side of esophagus and attaching dorsal to anterior adductor muscle. Posterior pedal retractors vertically passing dorsally from base of foot and attaching dorsal to posterior adductor muscle. Ctenidia thick, dark, consisting of two demibranches, equal in width and thickness (sometimes the outer demibranch slightly smaller than the inner). Labial palps forming small triangular extensions of anterior margins of proximal oral groove, lying close to antero-ventral corner of gill. Mouth wide, situated posteriorly on mid-dorsal line of anterior adductor muscle. Esophagus extending along dorsal side of anterior retractor muscle. Stomach divided into two parts: anterior—elongated and narrow; posterior—short and globular. Two ducts of digestive diverticula opening into anterior stomach compartment. Short combined midgut-style sac (though no style detected) extending posteriorly. Hind gut forming an anterior loop dorsal to mid gut, running anteriorly, then turning dorsally and passing through the heart and running posteriorly dorsal to kidney and posterior adductor muscle, opening at ventral side of posterior adductor muscle (food remains present in hind gut and stomach). Digestive diverticula and gonad forming a single large mass penetrated by a complex system of ciliated ducts. Kidneys large, elongate, unlobed sacs, occupying a postero-dorsal position between posterior adductor muscle and heart. Heart triangular, lying between kidney and dorsal margin of digestive diverticula.

Figures 2–9. *Conchocele bisecta* (Conrad, 1849), west coast of Kamchatka, Sea of Okhotsk (57°02'N, 152°29'E), 482–491 m. Figures 2, 3. Right valve, length 152.5 mm. Figures 4, 5. Left valve, length 152.5 mm. Figure 6. Dorsal view of both valves. Figure 7. Posterodorsal view of both valves. Figure 8. Anterior view of both valves. Figure 9. Organs of the mantle cavity as seen from the right side with shell and mantle removed. Key: A—anus; AA—anterior adductor muscle; CT—ctenidia; DGG—digestive gland and gonad; F—foot; K—kidney; L—ligament; LP—labial palp; M—mantle; PA—posterior adductor muscle.





Figures 10–21. *Conchocele bisecta* (Conrad, 1849). Figures 10–15. West coast of Kamchatka, Sea of Okhotsk ($55^{\circ}00'2''N$, $154^{\circ}06'3''E$), 522–531 m. Figures 10, 11. Right valve of young specimen, length 46.8 mm. Figures 12, 13. Left valve, length 78.9 mm. Figures 14, 15. Left valve, length 127.9 mm. Figures 16, 17. Paramushir Island, Sea of Okhotsk ($50^{\circ}30.88'N$, $155^{\circ}18.14'E$), 792–804 m, right valve, length 77.5 mm. Figures 18, 19. Sea of Japan ($42^{\circ}19.6'N$, $131^{\circ}10.6'E$), 130 m, right valve, length 133.3 mm. Figures 20, 21. Kyushu-Palau Ridge, Pacific Ocean, left valve, length 131.3 mm.

Variability: Shell shape and proportions distinctly change with age (Table 1). In young specimens (up to 50–70 mm), in contrast to adults, the shell is much thinner, more rounded, and less convex; the apical angle is larger; the beaks are more prominent; the anterior shell margin is concave; the lunule is less expressed; the nymph is shorter; and the anterior muscle is more vertical

(Figures 10, 11). Moreover, in young specimens the mantle is thicker, the posterior part of stomach is not globular, kidneys and digestive diverticula are smaller, the ducts of digestive diverticula are shorter, and the tubules branch off almost immediately. In adult specimens the shell shape and proportions also vary significantly. Shell height, width, and apical angle vary. Some specimens

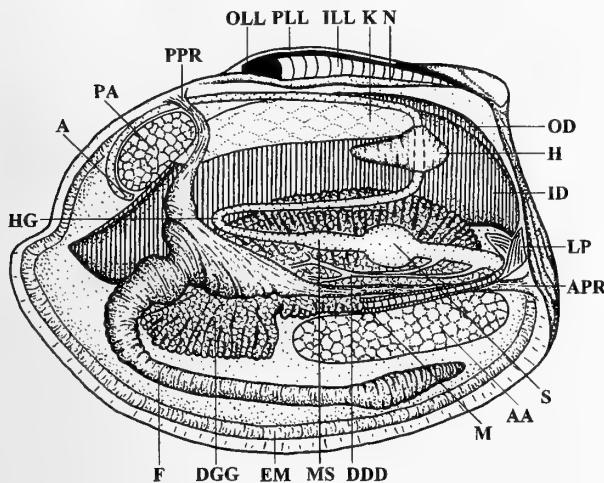


Figure 22. *Conchocele bisecta* (Conrad, 1849) (specimen from west coast of Kamchatka, Figures 2–9): internal morphology as seen from the right side with the right ctenidium and digestive diverticula removed. Key: A—anus; AA—anterior adductor muscle; APR—anterior pedal retractor muscle; DGG—digestive gland and gonad; EM—edge mantle; F—foot; H—heart; HG—hind gut; ID—inner demibranch; ILL—inner layer of ligament; K—kidney; LP—labial palp; M—mouth; MS—mid gut and style sac; N—nymph; OD—outer demibranch; OLL—outer layer of ligament; PA—posterior adductor muscle; PLL—periostracal layer of ligament; PPR—posterior pedal retractor muscle; S—stomach.

have a rather elongated shell. Many exhibit a concave anterior shell margin (Figures 12, 13). This is especially characteristic of specimens from the southern Sea of Okhotsk and the Sea of Japan (Figures 18, 19). All of these specimens have a concave anterior shell margin. In addition, *C. bisecta* from the Sea of Japan is distinguished by a far thicker shell, a wider and longer nymph, and noticeably wider anterior and posterior adductor scars (Table 1). Variable anatomical features are relative length of the foot and bulb form.

Remarks: Live individuals of *C. bisecta* were found in Puget Sound, Washington (Dall, 1892). Dall placed *C. disjuncta* in a synonymy of *C. bisecta* because he did not notice significant distinctive features between these species (Dall, 1895, 1901). However, in succeeding years many investigators regarded Recent *C. disjuncta* and *C. bisecta* as separate species (Tegland, 1928; Habe, 1964; Boss, 1967; Golikov & Scarlato, 1967; Keen, 1969; Bernard, 1972, 1983). Nevertheless, some American and Japanese researchers consider *C. disjuncta* to be a synonym of *C. bisecta* (Kanno, 1971; Abbott, 1974; Habe, 1977, 1981; Coan & Scott, 1997; Higo et al., 1999; Coan et al., 2000).

All the authors who thought *C. disjuncta* and *C. bisecta* to be separate species distinguished them only on the basis of shell morphology: different apical angles (larger in *C. bisecta*), a concave outline of the anterior surface and

the more prominent beaks in *C. bisecta*, larger sizes and more quadrate shell form in *C. disjuncta*. In addition, Bernard (1972) pointed to a number of anatomical differences between these species. Our studies showed that with regard to shell morphology and gross anatomy all large specimens from the Sea of Okhotsk were identical to *C. disjuncta* (Gabb, 1866; Nakazima, 1958; Okutani, 1962; Bernard, 1972), whereas young specimens were identical to *C. bisecta* (Conrad, 1849; Bernard, 1972). Moreover, some individuals had conchological features of both species. Hence, we believe that conchological and anatomical differences between *C. bisecta* and *C. disjuncta* are due to the age and individual variability of one species, *C. bisecta* (see “Variability” section).

For the recent fauna of Russia this species was erroneously stated as *Thyasira bisecta* (Conrad) solely on the basis of some finding of shell fragments at a depth of 20 m in Posiet Bay (southern Peter the Great Bay, Sea of Japan) (Golikov & Scarlato, 1967). Judging from fragments, the shell was about 70 mm high. Later on, this same material was presented as *Conchocele “disjuncta Gabb”* (Scarlato, 1981). However, in 1984 Ivanova & Moskaletz (1984) described a new species, *Conchocele scarlatoi* Ivanova & Moskaletz, 1984 (holotype shell length 70.9 mm) that was found approximately in the same region (Vityaz Bay, southern Peter the Great Bay) at a depth of 30 m. They stated that shell fragments found by Golikov & Scarlato (1967) in Posiet Bay belong to this species. However, Coan et al. (2000) considered *C. scarlatoi* to be a synonym of *C. bisecta*. We have examined fragments of shells from Posiet Bay, deposited at ZIN, as well as the type and supplementary material (different-aged individuals) of *C. scarlatoi* and also believe that this material represents one and the same, described as *C. scarlatoi*. As distinct from *C. bisecta*, different-aged individuals of this species have a triangular-angular shell, with an apical angle always less than 90°, a slightly convex anterior shell margin, extending dorsally; a straight posterior shell margin; and a well expressed lunule. All these features are rather stable and slightly prone to age and individual variation.

Distribution and habitat in the western Pacific: In the Sea of Okhotsk (Figure 23)—the northeastern Sea of Okhotsk (57°02'N, 152°29'E–57°16'8"N, 152°40'4"E); western Kamchatka (55°00'2"N, 154°06'3"E); Paramushir Island (50°30.88'N, 155°18.14"E) (Kuznetsov et al., 1987, 1989; Galchenko et al., 1988b; Kuznetsov & Levenstein, 1988); northeastern (54°28.5'N, 144°00.0'E; 54°22.5'N, 144°05.0'E; 53°24.0'N, 144°33.0'E) (Biebow & Hütten, 1999), (52°22'9"N, 144°38'4"E) and southeastern (45°53'2"N, 143°53'E; 47°14.8'N, 143°42.7'E) Sakhalin Island. In the Sea of Japan—the southern Primorje, Russia (42°19.6'N, 131°10.6'E); Chuetsu, Niigata Prefecture, Japan (37°48.6'N, 138°42.3'E) (Ito, 1989); Mishima, Yamaguchi Prefecture, Japan (35°27'N, 130°35'E) (Kanno,

Table 1

Conchoceles bisecta (Conrad, 1849). Shell measurements (mm) and indices: AA—apical angle; L—shell length, H—height, W—width, A—length of anterior adductor scar, P—width of posterior adductor scar, N—nymph length.

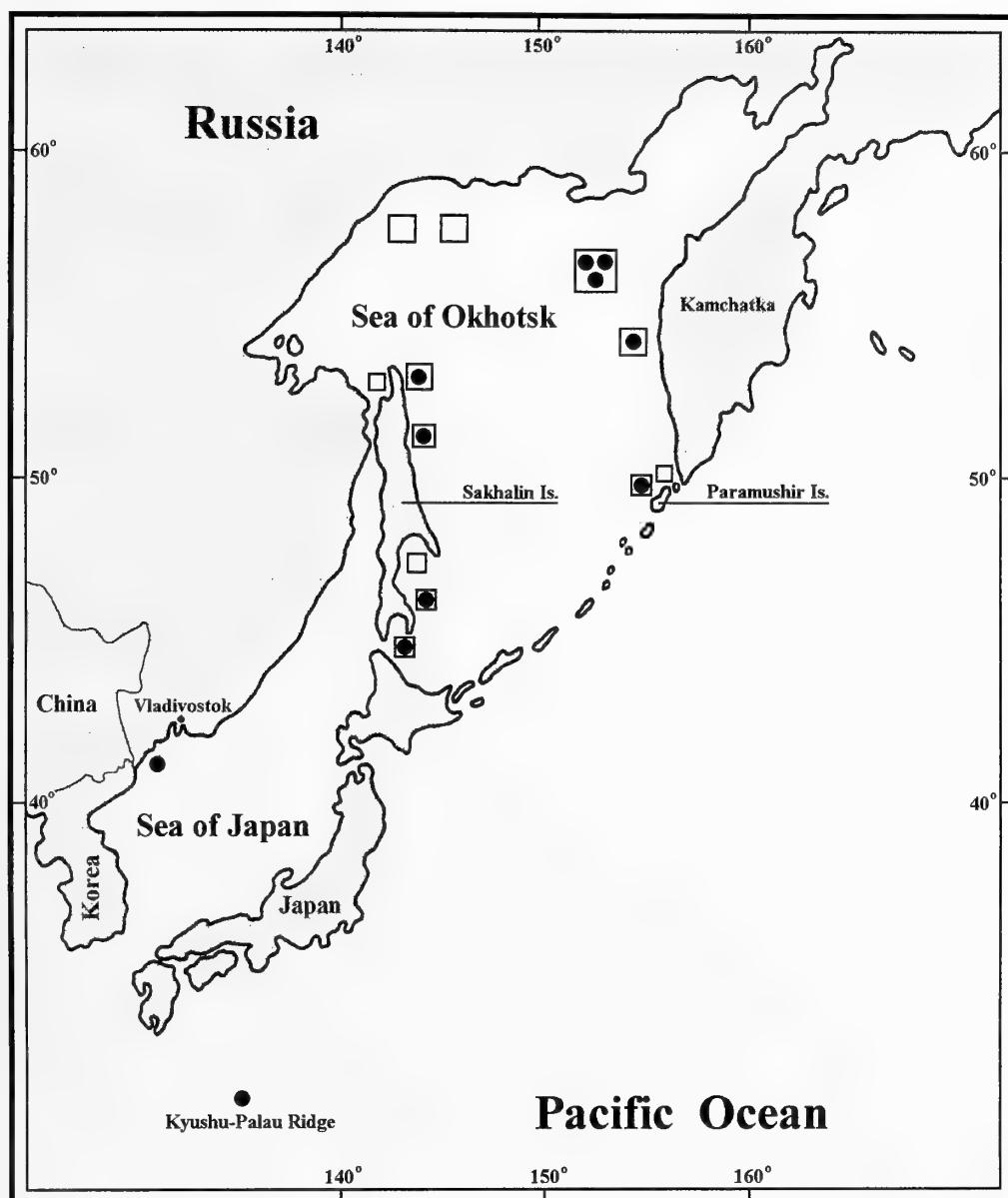


Figure 23. Map showing locations where *Conchoceles bisecta* was found (●) and distribution of cold-water methane-rich seep zones in the Sea of Okhotsk (□) (Obzhirov, 1993; Gaedcke et al., 1997; Biebow & Hüttner, 1999).

1971); Kasumi, Hyogo Prefecture, Japan ($35^{\circ}44'N$, $134^{\circ}38'E$) (Ito, 1967; Kanno, 1971); Oki Island and Shima Prefecture, Japan (Habe, 1958). In the Pacific Ocean near the coast of Japan—Cape Erimo, Hokkaido ($41^{\circ}40'N$, $143^{\circ}15'E$) (Kanno, 1971); Tosa and Sagami Bays (Okutani, 1962); Shikoku ($33^{\circ}10'N$, $133^{\circ}30'E$) (Habe, 1964, 1981; Kanno, 1971); south of Shikoku, Kyushu-Palau Ridge.

This species has been recorded at depths from 4 m to 1400 m (Higo et al., 1999). In the Sea of Okhotsk it was found at depths from 300 m (southeastern Sakhalin Is-

land) to 804 m (Paramushir Island) on silty sand and mud+ H_2S at a bottom water temperature of $1.65\text{--}2.2^{\circ}C$. Near Paramushir Island this species was registered in a zone of methane-rich fluids with concentrations of dissolved methane in bottom water from 180 nL/L to 1000 nL/L at a “normal” bottom-water methane background of 30–40 nL/L (Obzhirov, 1993; Gaedcke et al., 1997). Near the northeastern Sakhalin Island, this species was registered from 385 to 750 m in zones of gas seepage with concentrations of dissolved methane in bottom water from 446 nL/L to 11,076 nL/L (Biebow & Hüttner, 1999);

in the Sea of Japan—from 130 m (southern Primorje, Russia) to 350 m (Kasumi, Hyogo Prefecture, Japan) on silty sand and mud at a bottom-water temperature of 1.5°C (Kanno, 1971); in the Pacific Ocean off Japan—from 200 m (Cape Erimo) to 770 m (Sagami Bay) at a bottom-water temperature 2.0–9.8°C (Okutani, 1962; Kanno, 1971). This species was also recorded near Japan at depths of 4 m and 1400 m (Habe, 1977; Higo et al., 1999).

DISCUSSION

As mentioned before, *C. bisecta* dwelling near methane-rich seeps off Paramushir Island has a dual feeding type: suspension feeding and bacterial symbiotrophy. Large amounts (up to $n \cdot 10^9$ per 1 gram wet mass) of intracellular methane- and sulfur-oxidizing symbiotic bacteria were found in the gills of this species (Galchenko et al., 1988a, b; Strizhov et al., 1990; Kuznetsov et al., 1991). It was also shown that bacterial methane-oxidation prevailed significantly over CO₂ fixation. The share of methane carbon in total carbon, assimilated in methane-oxidation and CO₂ fixation, is 68–76% (Galchenko et al., 1988b). Large mollusk size, high population density near methane-rich seeps (up to 15–20 ind/m² at a biomass no less than 2.5–3.0 kg/m² (Kuznetsov et al., 1987, 1989)), and bacterial symbiotrophy as the main feeding mode enabled Kuznetsov et al. (1987, 1991) to conclude that this species is a typical representative of a highly specialized “specific” fauna of methane seeps, analogous to different species of the genus *Calyptogena* Dall, 1891.

Zones of cold-water methane/sulfide seeps and the associated fauna have been studied in many areas of the Pacific Ocean: subduction zones off Oregon (Suess et al., 1985); Japan (Tenryu Canyon, Japan and Kurile trenches) (Juniper & Sibuet, 1987); and Peru (Olu et al., 1996); Laurentian Fan, Canada (Mayer et al., 1988); Sagami Bay, Japan (Okutani & Egawa, 1985); continental slope off northern California (Kennicutt et al., 1989); Monterey Bay, Southern California (Orange et al., 1994). However, *C. bisecta* was not recorded as a member of cold seep communities in these areas. Nevertheless, a comparison of our materials with the results of geological and gas-chemistry research in the Sea of Okhotsk has shown that *C. bisecta* was found in the Sea of Okhotsk only in areas of cold-water seeps (Figure 23) with abnormally high concentrations on methane (10 times the background ones) in bottom water and sediments (Obzhirov, 1993; Gaedicke et al., 1997; Biebow & Hüttén, 1999). In the bottom sediments close to the gas vents, gas hydrates were found. This suggests that gas hydrates are a source of emanating gas.

It is noteworthy that the shelf and bathyal zones of western Kamchatka were repeatedly examined by expeditions of PRIFO. Bottom trawling at a depth over 100 m was carried out in 1997 and 1998 by two different

expeditions. Nevertheless, both expeditions found shells and live specimens of *C. bisecta* only in the area corresponding to methane anomaly in bottom water and sediment.

There are vast zones of cold-water methane seeps with gas hydrates in the bottom sediments on the shelf and the bathyal zones of northeastern Sakhalin Island (Obzhirov, 1993). In some zones (Giselle Flare, Obshirov Flare, and Piltunsky Flare), at depths of 385–750 m, large aggregations of shells and live specimens of *Conchocele* sp. were found with the help of video-/camera-sled OFOS (Ocean Floor Observation System) (Biebow & Hüttén, 1999). Our studies of valves from these areas have shown them to be *C. bisecta*. It is characteristic that populations of *C. bisecta* resemble narrow strips or spots depending on the form of active methane seepage zones (Obzhirov, personal communication).

Perhaps, in other areas of the Pacific and Atlantic oceans *C. bisecta* also occurs in areas with a high concentration of methane in the bottom sediment. *C. bisecta* was recorded in Sagami Bay, which is characterized by the abundance of cold-water methane seep zones with dense aggregations of different species of the genus *Calyptogena* (Okutani, 1957; 1962; Okutani & Egawa, 1985; Kojima & Ohta, 1997). Also, a species of the genus *Conchocele* with methane-oxidizing symbiotic bacteria was found in the area of hydrothermal vents of Guaymas Basin, the Gulf of California (Galchenko et al., 1988a, b). This species was found in those areas of Guaymas Basin where no traces of recent hydrothermal activity were noted but which had a high methane content in the sediments. Boss (1967) showed that *C. bisecta* was found in Gulf of Darien (Caribbean Sea) in a dredging station together with *Calyptogena* sp., later described as *Calyptogena (Ectenagena) modioliforma* (Boss, 1968) (Boss & Turner, 1980). The presence of a species from the genus *Calyptogena* in this station attests to the presence of hydrothermal vents or cold-water methane/sulfide seeps in this area.

Zones with high dissolved methane concentration in sediments and bottom water are widespread in the world's oceans (Grassle, 1986; Hovland & Judd, 1988) and are favorable for the life of various animals, containing sulfur- and methane-oxidizing endosymbiotic bacteria. This may account for the fact that *C. bisecta* has such a wide geographic distribution and a large depth range. Taking into account the very large size of *C. bisecta* and the considerable contribution of the methane- and sulfur-oxidizing bacteria to the nutrition of mollusks, we conclude that *C. bisecta* may dwell only in organic-rich sediments with high total methane and sulfide concentrations which are specific to cold-water methane-rich seeps. Here it forms dense aggregations and may be indicative of high methane concentration in bottom sediments connected with the location of seeps.

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Walter B. Miller (1918–2000): Molluscan Taxa and Bibliography

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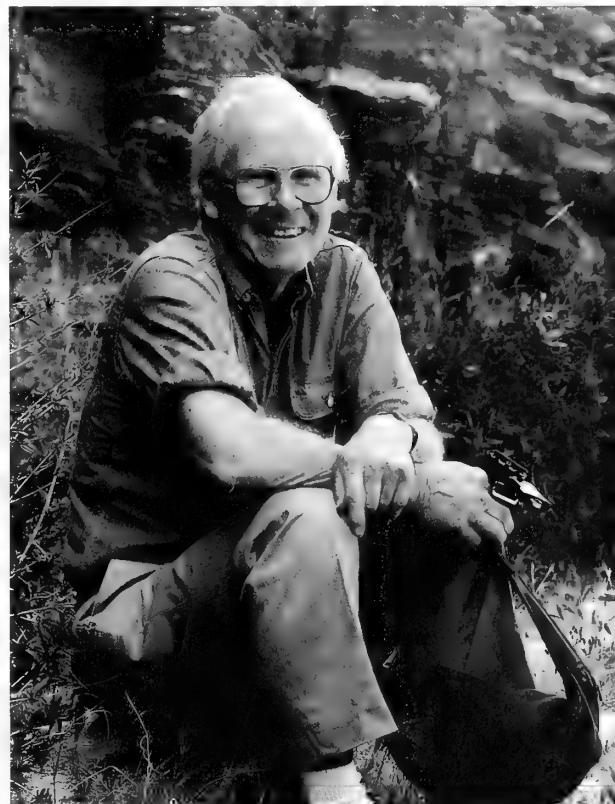
Walter Bernard Miller, Professor Emeritus of Biology at the University of Arizona and Research Associate of the Department of Invertebrate Zoology, Santa Barbara Museum of Natural History, passed away on July 10, 2000, at his home in Lompoc, California.

Miller was born in Paris, France, on August 23, 1918, three weeks after his father, an American aviator in the Lafayette Escadrille, had been shot down and killed during the battle of Chateau-Thierry. His mother, a French woman, brought him to the United States in 1929. He lived in South Carolina and attended The Citadel and the United States Naval Academy, graduating from the latter in 1949. During World War II, he piloted dive bombers in numerous combat missions in North Africa and the Pacific. On orders from the Navy, in 1945 he obtained a Master's degree in aeronautical engineering from the California Institute of Technology.

After retiring from naval service, Miller worked in civilian technology for four years before choosing to follow his avocation as a naturalist and entering the University of Arizona, where he obtained a Ph.D. in biology in 1967. His doctoral dissertation, *Anatomical revision of the genus Sonorella (Pulmonata: Helminthoglyptidae)*, established his expertise in the preparation and study of land snail reproductive systems, a specialty he would pursue until the end of his career. The results of his collecting (but, unfortunately, not his anatomic findings) were published in *The Mollusks of the Arid Southwest, with an Arizona Check List* (1973), co-authored with Joseph Charles Bequaert.

Following a postdoctoral year at the University of California's Bodega Marine Laboratory, he was hired by the University of Arizona as Assistant Professor of General Biology. Promoted to Associate Professor in 1972 and Professor in 1977, he oversaw the work of numerous graduate students. Doctoral study under Walt Miller invariably included field work in the American Southwest, where, under sometimes arduous conditions, his students collected specimens to be reared in the lab, dissected, and analyzed. Insistence on involvement with one's material "from the ground up" was characteristic of his method, and he would rarely describe a new species that he had not personally collected, even if ample material already existed in museum collections.

Required by the university to retire at age 70, in 1988 Miller moved to California with his wife, Betty Sue. Set-



Walter Bernard Miller, Santa Catalina Mountains, Arizona, April 1987. Photograph by Lance H. Gilbertson.

tling first in Santa Barbara, they later built their dream home in Lompoc. As a Research Associate of the Santa Barbara Museum of Natural History, he continued field work and publication on western North American pulmonate land mollusks. There his primary focus changed from Helminthoglyptidae to Polygyridae, and he began the task of documenting previously unsuspected diversity in species of *Vespericola* in the Pacific Northwest. His extensive personal collection of land snails and anatomical preparations was donated to the museum in 1991.

It was typical of Miller's generous spirit that he often named new taxa for his co-authors and students. Colleagues have returned the compliment with these taxon names: *Sonorella milleri* Christensen, 1981; *Millerelix* Pratt, 1981; *Xerarionta walmilleri* Roth, 1984; *Helminthoglypta milleri* Reeder, 1986.

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NOTES, INFORMATION & NEWS

Non-Polar Components of Prey Sponge Extract Attract *Rostanga pulchra* (Nudibranchia: Doridacea)

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Introduction

Opisthobranchs that lack the physical protection of a shell require other anti-predator defenses such as noxious chemicals or crypsis (Thompson, 1976). *Rostanga pulchra* MacFarland, 1905 mimics the color of its sponge prey almost perfectly by sequestering non-polar carotenoid pigments in the same proportions as found in several prey sponges (*Opheliaspongia pennata*, *Esperiopsis originalis*, and *Plocamia karykina*; Anderson, 1971). Yet *R. pulchra* often moves between patches of sponge and feeds on several different species (Anderson, 1971); how does a slug find sponges containing the compounds needed for crypsis?

Many gastropods detect prey chemically (Sakata, 1989), and this capability is known for *R. pulchra* and some other dorid nudibranchs (Cook, 1962; Anderson, 1971; Elvin, 1976). It would seem adaptive if nudibranchs were attracted to prey via the same compounds they sequester. Indeed, the nudibranch *Tambja eliora* is attracted to tambjamines A and B, compounds it sequesters from its prey *Sessibugula translucens* (Carté & Faulkner, 1986). However, these compounds are fairly polar, whereas most nudibranch-sequestered compounds are non-polar (Avila, 1995) and relatively insoluble in water. Non-polar attractants are known for some herbivorous gastropods, but no attractive non-polar prey compounds are currently known for carnivorous gastropods (Kohn, 1961; Audesirk & Audesirk, 1985; Sakata, 1989).

Therefore, we used a Y-maze design to test whether *R. pulchra* is attracted to: (a) whole sponges, (b) sponge extracts (dissociated compounds), and (c) the non-polar fraction of sponge extracts, which includes carotenoids.

Methods

Collections

Thirty *Rostanga pulchra* (4–15 mm in length) and several rocks with *Opheliaspongia pennata* were collected intertidally or by SCUBA from Barkley Sound, British Columbia in October and November 1998, and kept in running natural seawater at Bamfield Marine Station. Nudibranchs were kept in individual mesh-sided containers upstream from rocks with sponges, and fasted for 6–18 days before being tested.

Extracts

Sponges were scraped from rocks and thrice extracted with three times volume of methanol for 24 hr each time. This extract was divided, half for the whole extract assays, and half for the non-polar extract assays. The latter half was extracted in a separatory funnel three times with an equal volume of hexane, and all three hexane portions combined as “non-polar extract.” Both extracts were reduced to 2.5 mL in a rotary evaporator at $\leq 35^{\circ}\text{C}$. For the assays, whole extracts were contained in 7% agar blocks, but 8.5% agar was required for non-polar extracts and controls to solidify.

Y-Maze Assays

We assayed responses of *R. pulchra* in a Y-maze of clear, nonporous plexiglass (36 × 10 cm, with arms 21.5 × 10 cm). Flows were balanced between arms using dyes, and were equivalent for each test. Treatments (sponge, whole extract, non-polar extract) were randomly assigned to arms for each assay, and seawater run through the apparatus for several minutes, allowing compounds to diffuse. Nudibranchs were then placed in the middle of the Y-maze and allowed to crawl freely. We recorded a “choice” if the nudibranch progressed more than two body lengths into either arm, and “no choice” if it had not entered either arm after 30 min. After each trial, the Y-maze was emptied of water and scrubbed to remove mucus trails. Each nudibranch was tested once against sponges, whole extract, and non-polar extract sequentially; we feel this non-random order did not affect the significance of the results. For statistical analysis, we excluded “no choice” animals within each experiment, and used a contingency table (χ^2 test with continuity correction; Zar, 1984) to determine whether the stimulus position significantly affected the side of the Y-maze chosen by the slug.

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Table 1

Responses of *Rostanga pulchra* to *Opheliaspongia pennata* treatments in a Y-maze. Treatment vehicles were rocks for sponges and agar blocks for extracts; controls for each treatment were bare rocks or agar blocks with solvent only. Significant differences in slug position were tested via χ^2 tests with continuity correction. See Methods section for details.

Treatment	Stimulus position	Slug position		χ^2	<i>P</i>
		Left	Right		
Whole Sponge	Left	10	1	5.860	0.016
	Right	3	7		
Sponge Extract	Left	11	2	4.868	0.027
	Right	4	8		
Nonpolar Fraction	Left	12	0	7.106	0.008
	Right	4	6		

Results

Approximately 80% of the nudibranchs chose the treatment arm in each experiment. The stimulus position significantly affected which arm the slug chose (Table 1). The slugs also preferred the left arm of the maze, possibly due to slight differences in the flow rate. Allocation of treatments to each arm was roughly 50%.

Discussion

R. pulchra is attracted to whole *O. pennata*, confirming the results of Cook (1962) and Anderson (1971). In Anderson's assays, it is interesting that *R. pulchra* was not attracted to *E. originalis*, another prey sponge containing the correct mix of carotenoids; this may be due to the motivation of the animals, or the arena she used. *R. pulchra* also responds to isolated compounds from this sponge, suggesting that chemotaxis is an important means of prey location for this nudibranch. Further, it responds to non-polar compounds at a level equivalent to that for whole extracts; to our knowledge, this is the first report of non-polar attractants for a carnivorous gastropod. The attractive compounds are possibly the sequestered carotenoids, as another nudibranch is attracted to the more polar compounds sequestered from its prey (Carté & Faulkner, 1986). If *R. pulchra* is attracted to these highly insoluble carotenoids, it would suggest extreme adaptation to detect at a distance the compounds sequestered from prey.

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Pseudorhaphitoma kilburni (Mollusca: Gastropoda: Turridae), New Species from Yemen, Red Sea

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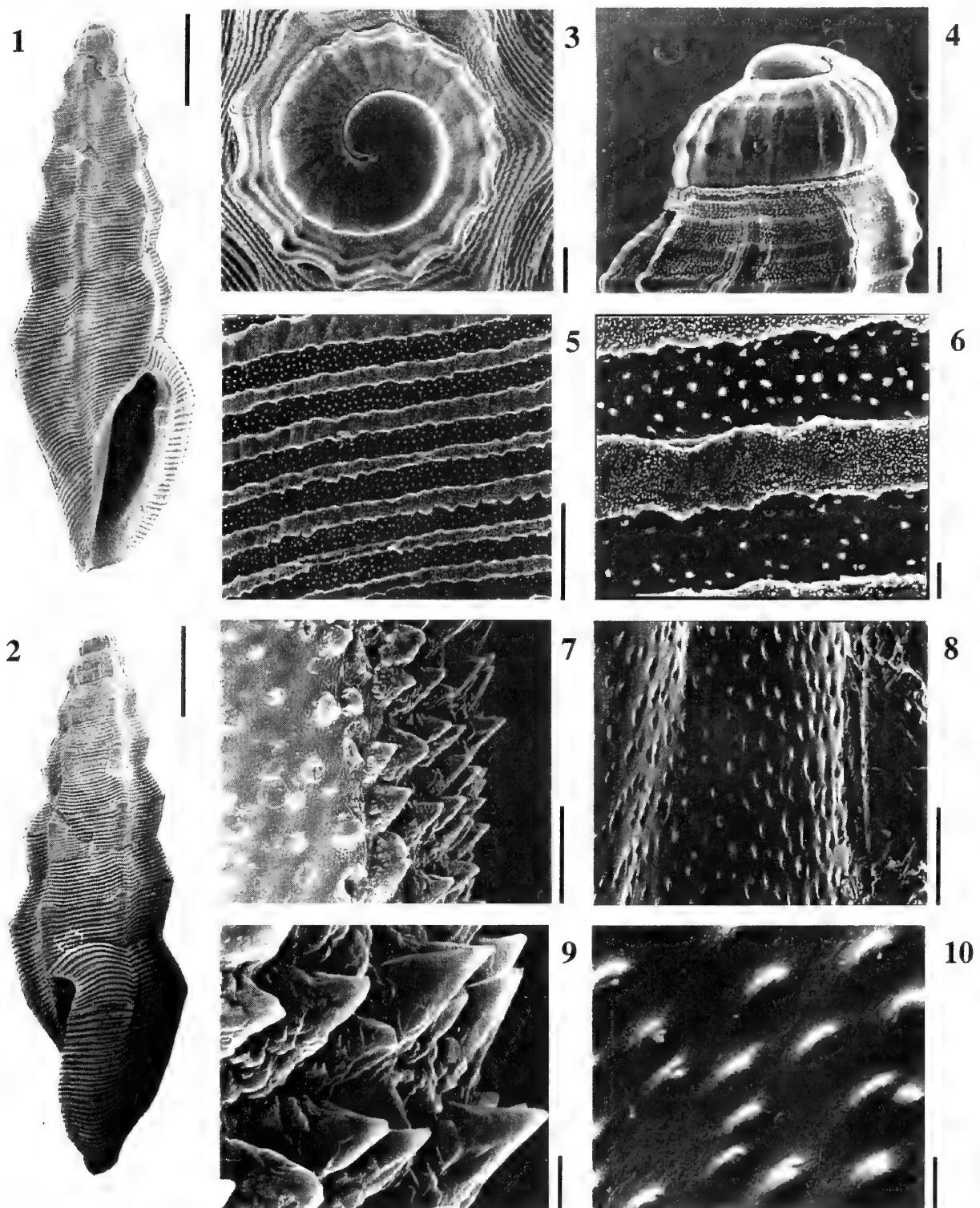
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Although the molluscan fauna of the Red Sea has been quite extensively investigated during more than two centuries, knowledge of the turrid fauna has remained rather poor. This work is intended to present the shells belonging to an unknown turrid species that have been sorted out from dredge samples collected during a marine survey in the Red Sea (Red Sed '92 European Community Project, September 1992, Gulf of Aden and South Red Sea, French oceanographic ship *Marion Dufresne*).

Almost all of the conchological characters of the present species are indicative of the mangeliine genus *Pseudorhaphitoma* Boettger, 1895; nevertheless, they are quite distinct from *Pseudorhaphitoma iodolabiata* (Hornung & Mermod, 1928), the only *Pseudorhaphitoma* previously known from the Red Sea, and those of any other de-



Figures 1–10. *Pseudorraphitoma kilburni* Morassi & Bonfitto, sp. nov. Figures 1, 2. Holotype MZB 12757; scale bar 1 mm. Figures 3, 4. Protoconch; scale bar 100 µm. Figure 5. Microsculpture of teleoconch; scale bar 100 µm. Figure 6. Microsculpture of teleoconch; scale bar 10 µm. Figure 7. Portion of labial callus; scale bar 50 µm. Figure 8. Interior part of outer lip; scale bar 50 µm. Figure 9. Parietal prickly nodules; scale bar 10 µm. Figure 10. Pustules of interior part of outer lip; scale bar 10 µm.

scribed species particularly *P. stipendiarii* Kilburn, 1993, from Southern Africa, which this species resembles.

In this paper we have hesitantly used the traditional classification rather than that proposed by Taylor et al. (1993). Rosenberg (1998) critiqued their methodology of analysis and showed that their results cannot be reproduced. Nevertheless, Taylor et al. (1993) recognized little anatomical evidence supporting the separation of the higher turrids from the Conidae.

Abbreviations: a/l = ratio of aperture length to total shell length; b/l = ratio of shell breadth to total length; AMSA = The Australian Museum, Sydney; ANSP = Academy of Natural Sciences of Philadelphia; BMNH = The Natural History Museum, London; MNHN = Muséum National d'Histoire Naturelle, Paris; MZB = Museo di Zoologia dell'Università di Bologna; NMSA = Natal Museum, Pietermaritzburg.

Family TURRIDAE H. & A. Adams, 1853

Subfamily MANGELILINAE, Fischer, 1883

Genus *Pseudorhaphitoma* Boettger, 1895

Pseudorhaphitoma Boettger, 1895 (as subgenus of *Clathurella*); Type species: *Mangelia fairbanki* G. & H. Nevill, 1875 (o.d.) *Turrella* Laseron, 1954

Type species: *Clathurella tenuilirata* Angas, 1871 (o.d.)

Pseudorhaphitoma kilburni Morassi & Bonfitto,
sp. nov.

(Figures 1–10)

Diagnosis: Shell mangeliine, with angular whorls sculptured with six sharp axial ribs continuous from whorl to whorl. Surface covered by thin spiral lirae with irregular edges, narrower than interstices. Eleven to 13 on first whorl; 17–23 on penultimate. Aperture narrow, outer lip with a rounded tubercle. Anal sinus U-shaped. Protoconch sculptured by axial riblets cut into nodules by four spiral ridges; maximum diameter 0.67 mm. Ground color pale-flesh; base and aperture whitish. Maximum length 6.1 mm.

Description: Shell moderately small for genus (4.1–6.1 mm), with a high, orthoconic spire and a distinctly produced, obliquely truncate base. Teleoconch of 4.5–5 whorls without shoulder. Suture shallow and slightly undulating. Whorls with a strong peripheral angle situated at or just below mid whorl, evenly convex anterior half and slightly concave shoulder slope. Aperture narrow, distinctly restricted into an embayment in its posterior end by the presence of parietal and labral nodules. Siphonal canal moderately short and wide, rather straight and shallowly indented, with its termination slightly obliquely truncate. Left side of base shallowly concave, not notched by rib intervals. Columella rather long and straight. Labial callus fairly thin, with rows of prickly

nodules in its interior part becoming blunted by abrasion exteriorly where they are somewhat vesicular in structure. Parietal callus filling posterior angle of aperture forming a feeble tubercle. Outer lip convex with a labral tooth just anterior to anal sinus and preceded by thick, varicoid rib. Edge of lip sharp, evenly arched, devoid of denticles, bearing, under strong magnification, microscopic, somewhat prickly pustules. Anal sinus deep for genus, symmetrically U-shaped, occupying most of shoulder slope. Axial sculpture of six strong ribs with sharply angular crests, continuous from whorl to whorl, and reaching on body whorl the base of siphonal rostrum. Ribs very weakly sinuous and opisthocline, much narrower in width than their interstices, which are wide and distinctly concave. Entire surface covered by thin, dense, tabulate spiral lirae, narrower or subequal in width to their interstices, bearing axially elongated plicles. Plicles fused together, giving edges of lirae very irregular nodose-pliculate appearance but not projecting laterally.

Spiral lirae sculptured by very numerous microscopic pores. Interstices between lirae with microscopic, spirally aligned granules. Peripheral angle characterized by presence of a main spiral lira, developed into a peripheral keel. Eleven to 13 lirae present on first teleoconch whorl; 17–23 on penultimate; base of body whorl with about 30–35 lirae. Ground color pale-flesh; base and aperture whitish. Protoconch bluntly conical, of about 1.6–2 whorls (termination not well defined) with rather deep suture. First whorl distinctly flattened but initially projecting sideward, second convex. Sculpture consisting of arcuate, orthocline axial riblets cut into rounded granules by four spiral ridges of which the median is the strongest. Breadth: 0.52–0.67 mm; height: 0.40–0.62 mm. Soft parts unknown.

Measurements (in mm):

	Length	Breadth	Aperture	b/l	a/l
Holotype	6.1	2.1	2.2	0.34	0.36
Paratypes	4.1–5.5	1.7–2	1.8–2	0.34–0.41	0.36–0.40

Type locality: Red Sea, offshore Yemen (14°46'72"N, 42°32'82"E), 76 m depth on muddy sand.

Type material: 27 adult and juvenile specimens from type locality. Holotype: MZB 12757, Paratypes: 21 MZB 12758; 1 AMSA; 1 ANSP; 1 BMNH; 1 MNHN; 1 NMSA L4787/T1577.

Etymology: Named after Dr. R. N. Kilburn of the Natal Museum in recognition of his substantial contribution to our knowledge of the Turridae s.l.

Discussion: *Pseudorhaphitoma* Boettger, 1895, was originally introduced as a subgenus of *Clathurella* Carpenter, 1857, with *Mangelia fairbanki* G. & H. Nevill, 1875, from Bombay, as the type species. Subsequently, Hedley (1922) in his revision of the Australian turrids regarded

Pseudorhaphitoma as worthy of full generic status, whereas Thiele (1925) used it as a subgenus of *Mangeliella* Risso, 1826. Wenz (1943) reported the genus under the incorrect spelling of *Pseudoraphitoma*, followed in this by all modern turrid workers except Kilburn (1993). Laseron (1954:42) considered *Pseudorhaphitoma* a well defined genus because of its sculpture of axial ribs continuous from whorl to whorl. He also introduced the new genus *Turrella* for temperate water species from New South Wales and Tasmania. Powell (1966:107) noticed the resemblance between the genera but retained both as valid, and reported lists of characteristic species. More recently, Taylor et al. (1993:167) referred both taxa to the family Conidae. Kilburn (1993) synonymized *Turrella* with *Pseudorhaphitoma* and showed the presence, within the genus, of several intergrading types of spiral sculpture of the teleoconch and the protoconch. At present, the authors consider *Pseudorhaphitoma* as a rather heterogeneous assortment of at least 50 described species, ranging from the Indian Ocean to the Pacific Ocean, grouped together almost entirely on shell features, which are poorly defined. Very likely, when the anatomy of these species becomes known, a rearrangement of the complex will be necessary. At present, it is preferable to use *Pseudorhaphitoma* in a broad sense rather than erect new and doubtful genera or subgenera.

In its narrow form, acute axial ribbing, and well defined peripheral keel, the new taxon more closely resembles species of the western Atlantic genus *Ithycythara* Woodring, 1928, than any other described *Pseudorhaphitoma* species. However, as pointed out by Kilburn (1993), members of *Ithycythara* have a much finer spiral sculpture of microscopic striae and fewer basal threads.

Because of its rather characteristic protoconch (corresponding to "type C" of Kilburn, 1993) (Figures 3, 4) the species here described is referable to a small group of species represented by *Pseudorhaphitoma perlonga* (Melvill, 1899), *P. scitula* (E. A. Smith, 1884), and *P. stipendiarii* Kilburn, 1993. Among these, it could be reasonably confused only with the latter, described from Northern Zululand, South Africa, which it most closely resembles. From that species, *P. kilburni* sp. nov. can be separated by being smaller (4.1–6.1 mm versus 5.6–7.2 mm) and narrower (1.7–2.1 mm versus 2.1–2.3 mm) with a much stronger peripheral angle and a protoconch differing in shape and sculpture. In *P. stipendiarii*, the axial ripples of the protoconch are rendered strongly tuberculate by the spiral ridges, whereas in the new species, there are smaller rounded nodules. *P. kilburni* has a less dome-shaped protoconch. Regarding the spiral sculpture, *P. stipendiarii* differs in possessing spiral lirae that have distinctly serrulated edges (corresponding to "state 4" of Kilburn, 1993), whereas in *P. kilburni* the crests are irregularly nodose-pliculate ("state 3") (Figures 5, 6). Furthermore, *P. kilburni* bears fewer spiral lirae on the penultimate whorl (17–23 versus 27–33) and on the base

(30–35 instead of 40–50); the interstices between spiral lirae are much wider in the new species than in *P. stipendiarii*. The new species lacks denticles on the outer lip, whereas in *P. stipendiarii* there are approximately 14–16.

Finally, it should be noted that *P. stipendiarii* and *P. kilburni* are allopatric species, and no sign of intergrading is detectable in the type series of the latter, which shows a considerable degree of uniformity.

Under SEM, the new species was found to show a microsculpture of prickly granules in the interior part of the inner lip and prickly pustules in the interior part of the lip edge (Figures 7–10). These microsculptural elements have not previously been adequately figured and described. Judging from our SEM observations, similar granules are present within the family Turridae s.l. in several genera and even subfamilies. The systematic value of these micro features has not yet been adequately investigated. Their significance will probably be understood when enough species are known.

Acknowledgments. We thank Dr. R. N. Kilburn of the Natal Museum, Pietermaritzburg, South Africa, for comments and suggestions in preparation of this paper; one of the authors (AB) is grateful to Dr. Bruno Sabelli, Museo di Zoologia dell' Università di Bologna, and Dr. Marco Taviani, Consiglio Nazionale delle Ricerche (C.N.R.-Italian National Research Council), Bologna, Italy, whose help made his participation in a marine survey in the Red Sea possible; the crew of the French ship *Marion Dufresne* for their assistance during the trip, and the Centro Interdipartimentale per i Servizi Museografici d' Ateneo di Bologna (C.I.S.M.A.-Museum Services Center of University of Bologna) for financial support.

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**Diplommatina chaoi (Prosobranchia:
Diplommatinidae), A New Species from Southern
Taiwan**

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Introduction

The family Diplommatinidae Pfeiffer, 1856, is distributed in Asia, Europe, and Central America (Thiele, 1992). It comprises two subfamilies: Diplommatininae Pfeiffer, 1856, and Cochlostomatinae Tielecke, 1940 (Solem, 1959). Most of the species of Asian Diplommatinidae belong to the subfamily Diplommatininae. Nine of the 10 described species and subspecies of diplommatinines in Taiwan belong to the subgenus *Sinica* Moallendorff, 1885, of the genus *Diplommatina* Benson, 1849, and the other belongs to the genus *Palaina* Semper, 1865 (Kuroda, 1941; Pilsbry & Hirase, 1905).

Nine specimens of *Diplommatina* were collected in Pingtung County on 25 August 1997, and six in Taitung County on 27 August 1997 (Figure 1). Comparisons of morphological characters with other species revealed that the present specimens differ from all recognized species in the genus. This new species is described below.

Diplommatina (Benigoma) chaoi Hwang, Chang &
Chang, sp. nov.

(Figures 2–5, 7)

Description: The shell is minute, 3.67–4.44 mm long, dextral, turreted, and red-brown in color. The number of whorls is 7.5–8.75. The upper five whorls are slightly transparent. The first six whorls are strongly convex. The apex is concave in outline due to allomorphic expansion of the upper whorls. The penultimate whorl is the widest. The body whorl is slightly narrower than the penultimate whorl.

The first two whorls are embryonic whorls with smooth surfaces. The lower three-fourths of the third to fifth whorls is ornamented with thin, curved, axially lamellate ribs when unworn. There are 17 to 19 ribs on each ornamented whorl. The spaces between ribs vary on the three whorls from 0.16 mm to 0.27 mm in width, gradually becoming more widely spaced toward the fifth

whorl. The penultimate whorl and the first half of the body whorl are smooth, but have short, straight, oblique striae below the suture. The last half of the body whorl has very fine and dense striae (Figure 3). The umbilicus is closed. A transverse lamella (TL) is situated in the last whorl above the aperture on the outer wall (Figure 5). The upper end of the transverse lamella reaches the suture but does not extend farther onto the parietal wall. The first parietal lamella (PL1) is close to the suture, and the second parietal lamella (PL2) is close to the columella. The former is more elevated and longer than the latter. The first and second parietal lamellae reach a quarter of a whorl in length on the roof of the body whorl (Figure 7). A palatal plica is absent.

The aperture is subspherical. The peristome is thickened, expanded, and doubled, but not reflected. The parietal callus is thin. The columellar lamella is strong, pointed downward from aperture view, extended, and reaches half a whorl in length, not close to the transverse lamella, and slightly concave along its dorsal side (Figure 5).

The operculum is thin, semitransparent, and multispiral.

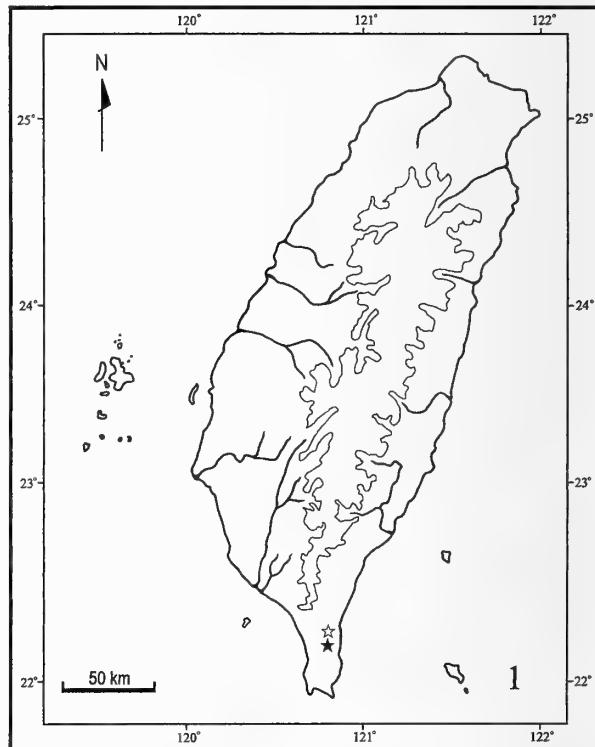
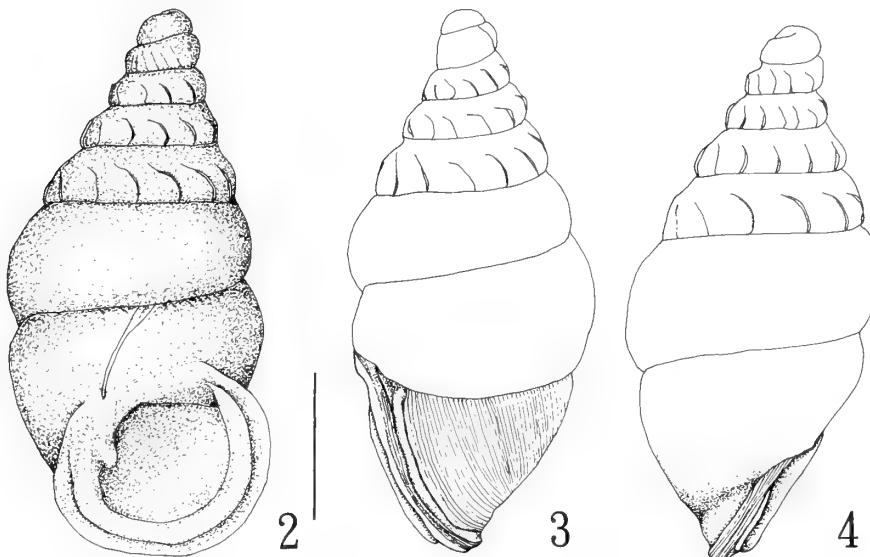


Figure 1. Map of Taiwan. ★ Type locality of *Diplommatina chaoi* Hwang, Chang & Chang, sp. nov. (Neiwen, Shihtzu, Pingtung County); ☆ Another locality (Kueitien, Dajen, Taitung County).

* Corresponding author



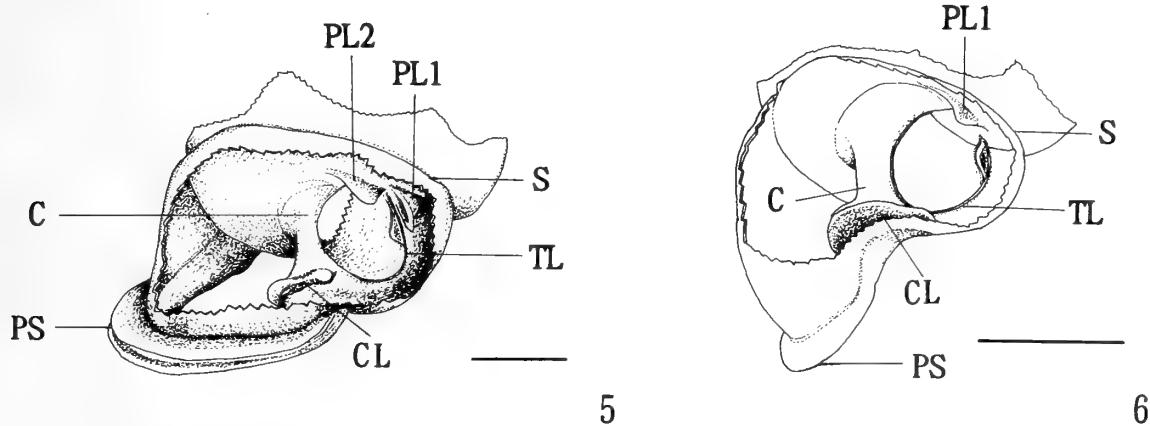
Figures 2–4. *Diplommatina chaoi* Hwang, Chang & Chang, sp. nov. Holotype, NMNS-002897-1. Figure 2. Apertural view. Figure 3. Right lateral view. Figure 4. Left lateral view. Scale line = 1 mm.

Measurements: The measurements of the holotype are: shell length 3.67 mm, shell width 1.76 mm, number of whorls 7.75. The measurements based on 15 specimens are: shell length 3.67–4.44 mm (average 4.01 mm), shell width 1.76–2.18 mm (average 1.98 mm), number of whorls 7.5–8.75.

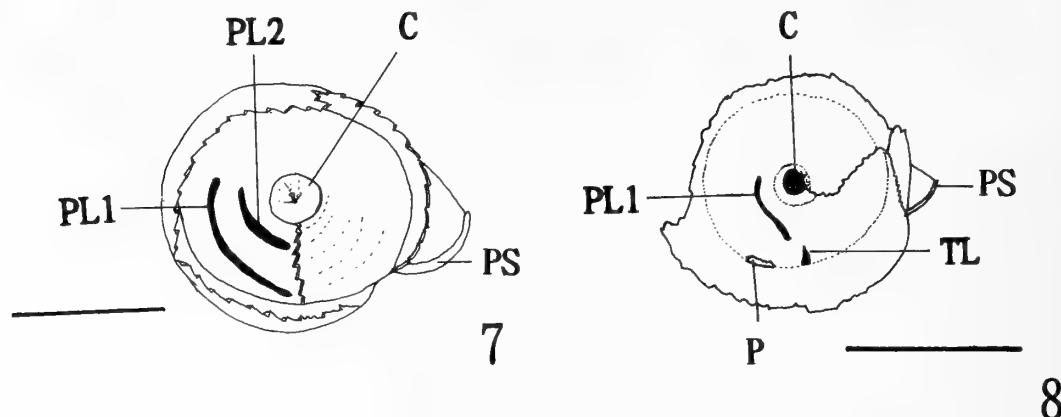
Type locality: Neiwen, Shihtzu, Pintung County, Taiwan (22°12'87"N, 120°50'61"E), altitude 330 meters. Nine specimens were collected by Chung-Chi Hwang on 25 August 1997.

Distribution: Type locality and Kueitien, Dajen, Taitung County (22°15'28"N, 120°49'73"E) (collected by David Chao and his associates on 27 August 1997).

Type materials: The holotype (NMNS-002897-1) is deposited in the National Museum of Natural Science together with four paratypes (NMNS-002897-2, 002897-3, 002897-4, and 002897-5). Four paratypes are deposited in the private collections of Chung-Chi Hwang, Kwan-Min Chang, Hsueh-Wen Chang, and Akira Tada, respectively.



Figures 5, 6. Figure 5. *Diplommatina chaoi* Hwang, Chang & Chang, sp. nov. A cracked specimen collected at type locality 15 December 1997. Upper left-side view with body whorl partially removed. Figure 6. *Diplommatina taiwanica*. Upper left-side view with body whorl partially removed. Abbreviations: C, columella; CL, columellar lamella; PL1, first parietal lamella; PL2, second parietal lamella; PS, peristome; S, suture; TL, transverse lamella; Scale line = 0.5 mm.



Figures 7, 8. Figure 7. *Diplommatina chaoi* Hwang, Chang & Chang, sp. nov. A cracked specimen collected at type locality 15 December 1997. Apical view of the lamellae (upper portion above body whorl has been removed). Figure 8. *Diplommatina taiwanica*. Apical view of the lamella (upper portion above body whorl has been removed). Abbreviations: C, columella; PL1, first parietal lamella; PL2, second parietal lamella; P, palatal plica; PS, peristome; TL, transverse lamella; Scale line = 1 mm.

Etymology: The species is named after Dr. David Chao (Department of Biological Sciences, National Sun Yat-Sen University) who offered his valuable specimens for this study.

Ecology: The nine type materials were collected in the litters of a ditch along a hillside. They were probably falling from the forest above. The forest is a secondary tropical monsoon forest. We tried to find any live individuals in the forest but in vain. The other six specimens collected in Taitung County were collected on the soil surface.

Remarks: The present new species differs from other known Taiwan *Diplommatina* species and neighboring areas in its turreted shell, lamellate ribs, and the lack of palatal plica. Therefore, it is assigned to the subgenus *Benigoma* Kuroda, 1928. Species of the allied subgenus *Sinica* possess a palatal plica. *Sinica* also is characterized by radula on the flat upper side of the lateral teeth (Ando, 1969). Live specimens of this new species were not collected, so that radular comparison was not available. All of the *Diplommatina* in Taiwan belong to the subgenus *Sinica*. Only two species, *D. oshimae* Pilsbry, 1901, and *D. pudica* Pilsbry, 1902, in Japan belong to *Benigoma* (Kuroda, 1963; Habe, 1943). This is the first record of *Benigoma* in Taiwan. The present new species differs from these two in its larger shell size, its smooth penultimate whorl, and the first half of the body whorl.

The lamellar morphology of *Diplommatina* of Taiwan has not been described. We selected a common species, *D. (Sinica) taiwanica* Pilsbry & Hirase, 1905 (collected from Feng-Huang-Ku, Nantou County) as a reference. The morphology of the columellar lamella is a useful character used in taxonomy at the specific level, and al-

lows comparison with that of *D. chaoi*. The columellar lamella of *D. taiwanica* closely approaches the transverse lamella, and smoothly extends without an indentation such as occurs in *D. chaoi* (Figures 5, 6).

Diplommatina taiwanica has only one parietal lamella (Figures 6, 8). This is the same as several Japanese species of the subgenus *Sinica* (Ando, 1968a, b). The second parietal lamella (Figures 5, 7) is an additional character found in this new species. The two parietal lamellae are situated on the parietal wall of the body whorl. However, the parietal lamella is rarely described. Further examination is needed to reveal the significance of the parietal lamellae for the subgeneric taxonomy of the genus *Diplommatina*.

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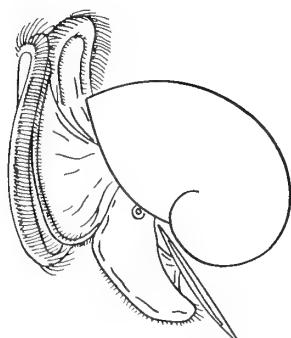
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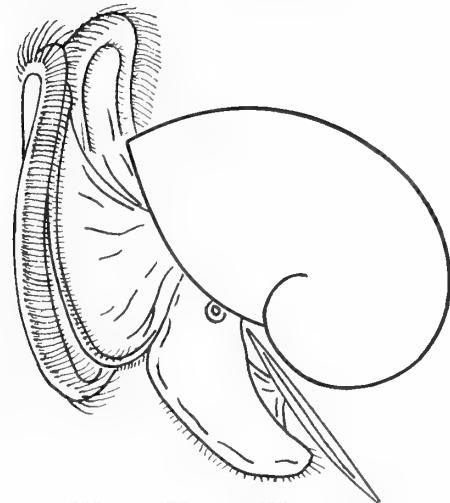
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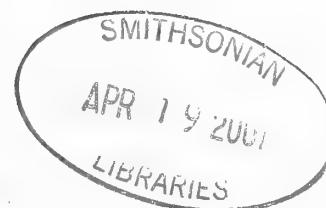


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Embryonic Stages of the Patagonian Squid *Loligo gahi* (Mollusca: Cephalopoda)

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Abstract. The embryonic development of *Loligo gahi* was observed from 4-day-old eggs to natural hatching. Egg strands spawned in the Valparaíso Bay, Chile, were transported to an open system tank for incubation. Temperatures ranged from 12.9°C to 13.5°C, salinities from 34‰ to 35‰, and the photoperiod was 12L:12D. The period from spawning to hatching ranged from 30–35 days. The diameter of individual eggs ranged from 2.5–3.2 mm, and the dorsal mantle length of hatchlings varied from 2.6–3.1 mm. The pattern of chronological appearance of organs was quite similar to loliginid species previously examined (*Loligo* aff. *gahi*, *Loligo bleekeri*, *Loligo pealei*, *Loligo vulgaris reynaudii*, and *Loligo forbesii*). However, *L. gahi* had a different (faster) development time and a smaller embryo and hatchling size than *L. bleekeri* (Japan) and *L. forbesii* (eastern Atlantic Ocean). Differences (heterochronies) among species are discussed. Allometric growth of embryonic development in *L. gahi* using seven morphometric parameters was undertaken.

INTRODUCTION

Loligo gahi d'Orbigny, 1835, is a neritic cephalopod distributed along the eastern Pacific Ocean from southern Peru to southern Chile, and in the south Atlantic from the Gulf of San Matías, Argentina to Tierra del Fuego, including the Falkland Islands (Roper et al., 1984; Hatfield & Rodhouse, 1994a).

Loligo gahi is one of the target species of the international cephalopod fishery of the Falkland Islands and Argentinean waters (Hatfield, 1996). This species is also caught by trawlers and the small-scale Chilean fisheries in Pacific waters, but it is minimally commercialized in the local markets. Although several studies about the biology and ecology of *L. gahi* have been carried out (e.g., Arancibia & Robotham, 1984; Carvalho & Pitcher, 1989; Hatfield, 1991, 1996; Guerra et al., 1991; Arkhipkin, 1993; Hatfield & Rodhouse, 1994a, b), there are some important aspects of its life cycle that remain unknown. The spawning grounds of this species have not been located, and its migratory pattern is not well known.

There are about 14 species of squid in the genus *Loligo* Lamarck, 1798 (Vecchione et al., 1998). However, embryological observations have been only undertaken in *Loligo pealei* Lesueur, 1821, *Loligo vulgaris* Lamarck, 1798, *Loligo opalescens* Berry, 1911, *Loligo forbesii* Steenstrup, 1856, *Loligo bleekeri* Keferstein, 1866, and *Loligo vulgaris reynaudii* d'Orbigny, 1845 (Harman & Gardiner, 1927; Arnold, 1965; Naef, 1928; Fields, 1965; Segawa et al., 1988; Hun-Baeg et al., 1992; Blackburn et al., 1998).

Two studies on the embryonic development and the hatching of *Loligo* aff. *gahi* (Barón, 1997a, b) based on egg masses collected from Golfo Nuevo (Argentina) in the Atlantic Ocean described the morphological changes of this species during its early stages of development. Also, Barón (1998) described morphometrics and chromatophore arrangement in the hatchlings of *Loligo* sp. from Argentinean Patagonia. However, this author indicated that the specific identity of these embryos is uncertain because both *L. gahi* and *Loligo sanpaulensis* Brakoniecki, 1984, have been reported to occur in the area.

Some authors (Nesis, 1987) maintain that the squid inhabiting the southwest Atlantic may be a different species (*Loligo patagonica* Smith, 1881). Although Brakoniecki (1986) indicated that *L. patagonica* is a junior synonym of *L. gahi*, we consider that it is necessary to undertake further morphological and genetic studies to confirm this issue.

This study shows the morphological form of the post-cleavage stages in the embryonic development of *L. gahi* from central Chile.

MATERIALS AND METHODS

The egg strings of *L. gahi* were collected from gill nets in Valparaíso Bay (33°2'S, 71°38'W, Figure 1) near the Montemar Marine Biological Station (MMBS). The nets were daily placed from 3:00 PM to 3:00 AM at 120 m depth. Twelve egg strings just spawned were carried in plastic containers with 10 L of seawater and taken to the

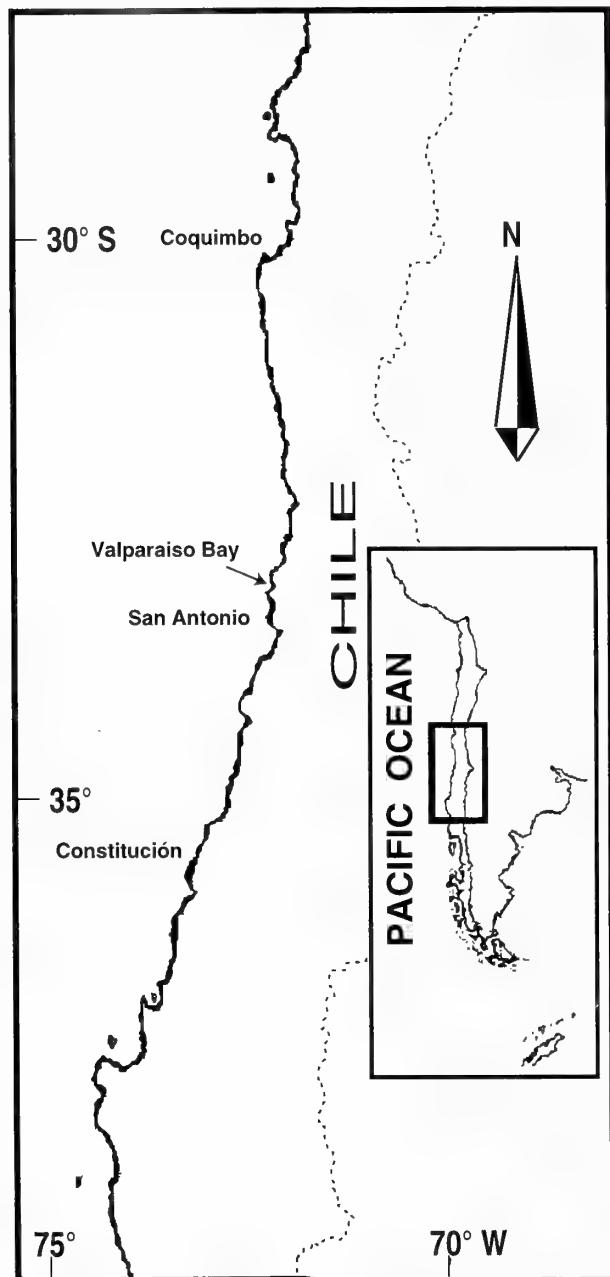


Figure 1. Location of collection of *Loligo gahi* egg masses.

open system tanks in the MMBs. The eggs were suspended in the water column and incubated at temperatures ranging from 12.9°C to 13.5°C and at salinities ranging from 34‰ to 35‰ during 35 days. The photoperiod was 12L:12D approximately. Daily observations were made from day 1 throughout the remainder of embryonic development until hatching in three egg strings with embryos of similar age. Representative living embryos were photographed daily and drawn to scale.

Table 1

Allometric growth of *Loligo gahi* during the embryonic development. ML: Mantle length in mm; HWI: Head width index; HLI: Head length index; EI: Eyeball index; MWI: Mantle width index; FLI: Fin length index; TLI: Tentacle length index. All indices are expressed as percentage of ML.

	15 days	20 days	30 days
ML	1.1	2.3	3.0
HWI	318.0	140.0	60.0
HLI	118.2	82.2	53.0
EI	86.4	41.0	23.3
MWI	181.8	104.0	90.0
FLI	63.6	48.9	40.0
TLI	86.4	48.0	46.7

The morphological staging criteria follow Arnold (1965) and they are represented in Arabic numbers. Roman numerals represent the stages proposed by Naef (1928).

Allometric growth of embryonic development was analyzed using the following morphometric indices: mantle length (ML) in mm; head width index (HWI); head length index (HLI); eyeball index (EI); mantle width index (MWI); fin length index (FLI); tentacle length index (TLI). All indices are expressed as percentages of ML.

RESULTS

The egg capsules were soft, gelatinous, and fingerlike in shape, their size ranging from 5 cm to 6 cm. Each egg capsule contained 50–60 eggs arranged in a spiral ($n = 12$). The size of the fresh eggs ranged from 2.5 mm to 3.2 mm in length ($n = 180$). The embryos hatched between 30 and 34 days, with the main hatching occurring on the 31st day. Figure 2 shows the developmental time of *L. gahi* from day 1 to hatching.

At the beginning of our observations (4 days after spawning), the eggs were at stage 13 (Arnold, 1965) or stage III–IV (Naef, 1928).

Pre-Organogenesis (Germ Layer Formation)

Day 4. Figure 3: Stage 13 (III–IV): Blastoderm covers 15–20% of the egg length. The border of the blastoderm is very distinct.

Day 5. Figure 4. Stage 14 (V): Blastoderm covers about one-half of the egg.

Day 6. Stages 15–15+ (VI–VII): Blastoderm covers about 70–75% of the egg. A shallow girdling depression appears around the equator forming a boundary between the future external yolk sac and the future embryonic body.

Table 2

Summary of egg size, development time, and hatching size in some *Loligo* species. 1, Summers (1983); 2, McMahon and Summers (1971); 3, Boletzky and Hanlon (1983); 4, Fields (1965); 5, McGowan (1954); 6, McConathy et al. (1980); 7, Barón (1997b); 8, Worms (1983); 9, Mangold-Wirz (1963); Boletzky (1974); 10, Blackburn et al. (1998); 11, Hun-Baeg et al. (1992); 12, Segawa et al. (1988).

Species	Egg size (mm)	Development time (days)	Hatching size (mm ML)	Temperature (°C)
<i>L. pealei</i>	1.1–1.6 ¹	10–27 ²	1.6 ³	12–23 ²
<i>L. opalescens</i>	2.0–2.5 ⁴	30–35 ⁵	2.5–3.2 ⁶	13.6 ⁵
<i>L. aff. gahi</i> ⁷	2.6–3.1	29–33	2.6–3.2	16.0 ± 4.0
<i>L. gahi</i>	2.5–3.2	30–35	2.6–3.1	12.9–13.5
<i>L. vulgaris</i>	2.3–2.7 ⁸	45–70 ⁹	2.7 ³	12–14 ⁹
<i>L. vulgaris reynaudii</i> ¹⁰	2.6–2.9	16–18	2.3–2.5	18.0 ± 1
<i>L. bleekeri</i> ¹¹	2.6–2.7	64–67	3.0–3.3	11.7 ± 0.4
<i>L. forbesi</i> ¹²	3.0–3.3	68–75	4.3–4.9	12.5 ± 0.5

Organogenesis

Day 10. Figure 5: Stage 16–17 (VII): Blastoderm covers about 70–80% of egg surface. Rudimentary optic vesicle primordia are visible as a disclike elevation. The primordia of arms and tentacles become visible. The shell gland primordium is conspicuous.

Day 11. Figure 6: Stage 17 (VII–VIII): The outer yolk sac envelope is nearly closed. The optic vesicle primordia are clearly distinguishable as two thickened placodes on either side of the embryo cap. The shell gland begins to invaginate as its border elevates. The mantle primordium is first visible surrounding the shell gland.

Day 12. Figure 7: Stage 18–19 (VIII–IX): The ocular globes are protruded and covered by a membrane. The primordia of statocysts become visible. The arms and tentacles are prominent. The shell gland is practically closed and the gill primordia become visible. The anterior and

posterior funnel fold primordia become visible. The optic vesicle is invaginated.

Day 13. Figure 8: Stage 20 (IX): Pore of the optic vesicle closed. The anterior and posterior funnel folds extend toward the midline. The sucker primordia first appear on tentacles. Shell gland invagination progresses. Gills prominent. Fin primordia become visible.

Day 15. Stages 21–22 (X–XI): Shell gland completely closed. Mantle covers two-thirds of the gills. Lens primordia are visible for the first time. Retina pigmentation is visible, and first differentiated suckers appear on tentacles.

Day 16. Figure 9: Stage 23 (XI–XII): Fins prominent. Mantle practically covers the gills. Retina pigmentation evident and cup-shaped. Anterior and posterior funnel folds fusing together. Gills clearly segmented. Statocysts completely formed and statoliths first visible.

Day 17. Figure 10: Stage 24 (XII): Funnel tube closed. Mantle covers the gills, but funnel retractor muscle is still visible. First red chromatophores appear on arms and tentacles.

Day 18. Stages 25–26 (XIII–XIV): The mantle covers the posterior margin of the funnel completely. Tentacular clubs with 17 suckers. Buccal mass faintly visible. Posterior lobes of internal yolk sac increase in size, but external yolk sac still longer than embryonic body. Ink sac becomes visible, but no ink is present. First chromatophores present in the surface of dorsal mantle.

Day 19. Figure 11: Stages 27 and 27+ (XVI–XVII): Hoyle's organ evident on posterior dorsal mantle between fins. Buccal mass and esophagus clearly visible. External yolk sac still slightly longer than embryonic body.

The buccal mass in embryos of *L. gahi* appears earlier than suggested by Figure 11 and the descriptions for stages 25–26 (XIII–XIV), but its formation can only be observed clearly from the dorsal side, which is not represented in the figures.

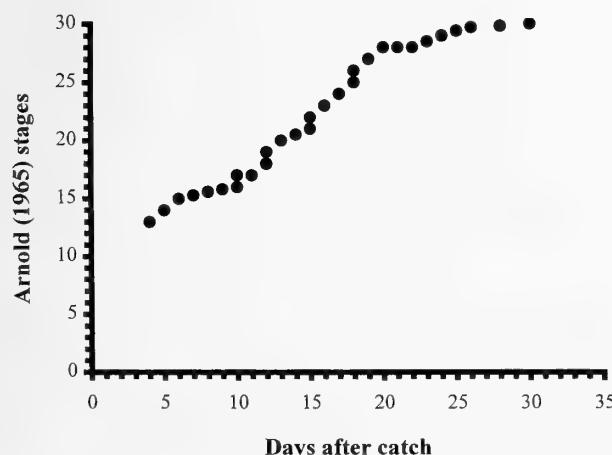


Figure 2. Embryonic development of *Loligo gahi* terms. Stages proposed by Arnold (1965) during the period from 4-day-old embryo to hatching.

Days 20–21–22. Stage 28 (XVIII): Chromatophores clearly present on dorsal and ventral mantle, ventral and dorsal head, arms, and tentacles. Four chromatophores on tentacle. Internal yolk sac approximately same size as mantle length. Primary lid covers the optic vesicle completely, and part of it is transformed into a cornea.

Days 24–25–26. Figure 12. Stages 29–29+–29++ (XIX–XIX+–XX): External yolk sac smaller than embryonic body and becoming progressively depleted. Anus and anal flaps are conspicuous and clearly visible. Posterior lobes of internal yolk sac forming small round bodies in the posterior part of the mantle. Four red chromatophores on each tentacle interspersed with three or four yellow ones. Stomach and caecum clearly visible. Ink sac filled with ink. At the end of these observations, mid-gut gland is clearly visible. Internal yolk sac much reduced in size.

Days 30–31. Figures 13, 14. Stage 30 (XX): Hatching.

Remaining external yolk sac dropped. Hoyle's organ depleted. Posterior lobes of internal yolk sac reduced to small round bodies. The number of ventral mantle chromatophores ranged from 40–58; the yellow ones were grouped in pairs, whereas the red ones were distributed in a more or less regular grid of oblique imaginary lines. The number of red chromatophores on the ventral side of the head ranged from 38 to 42. There were three to four red chromatophores on the right and left sides of each cheek. Four brown chromatophores were observed in the center of the dorsal side of the mantle, surrounded by eight yellow chromatophores located in the margins of the mantle. One hexagon of six brown chromatophores was found on the dorsal side of the head. Hatching size ranged from 2.6–3.1 mm ML ($n = 60$). Arm formula: III > IV = II > I.

Table 1 shows the allometric growth of the embryo based on the comparison between several morphometric indices measured at days 15, 20, and 30.

Based on the observed sequence of development of the major embryonic features, the developmental pattern of *L. gahi* was compared to that of *L. pealei*, *L. forbesii*, *L. bleekeri*, *L. aff. gahi*, and *L. vulgaris reynaudii* (Arnold, 1965; Segawa et al., 1988; Hun-Baeg et al., 1992; Barón, 1997b; Blackburn et al., 1998). The results of the comparisons are shown in Figure 15. *L. gahi* showed (Table 2) a different (faster) development time and a smaller

embryo and hatching size than *L. bleekeri* (Japan) and *L. forbesii* (eastern Atlantic Ocean).

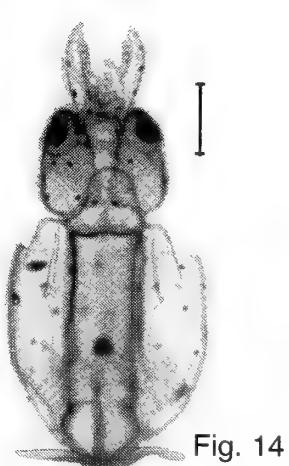
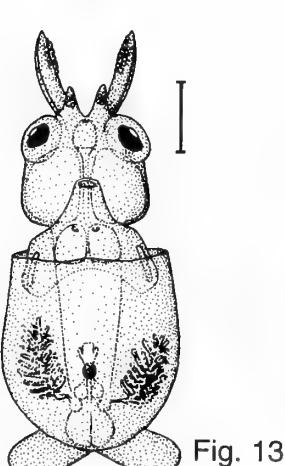
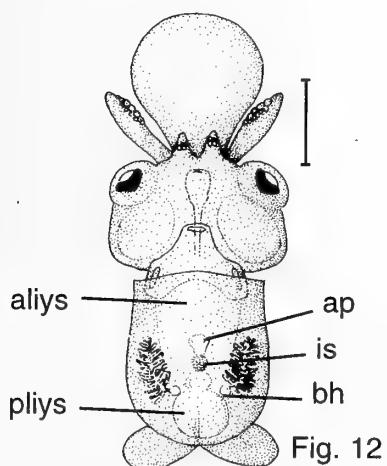
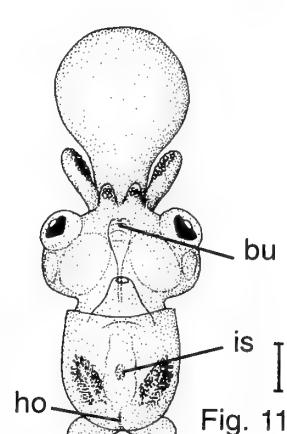
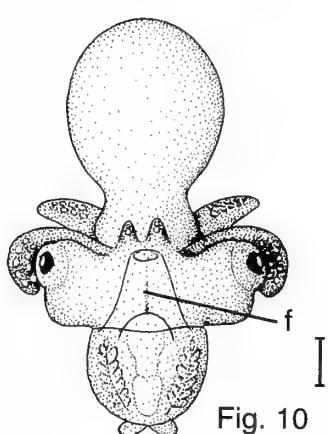
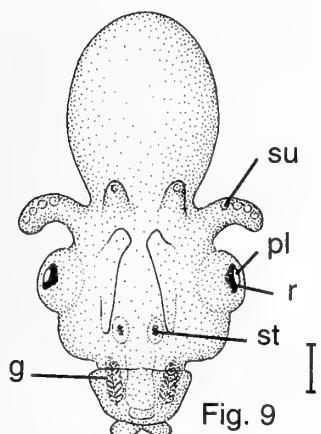
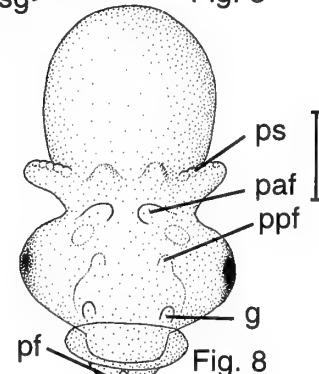
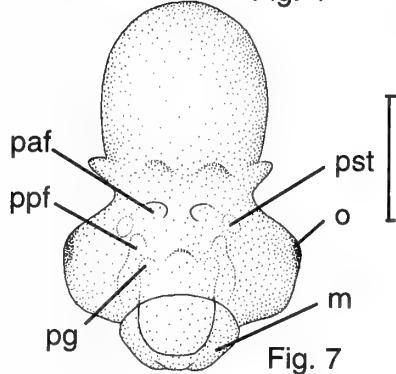
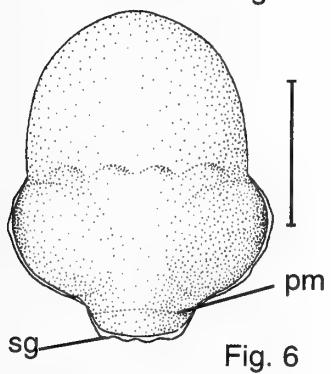
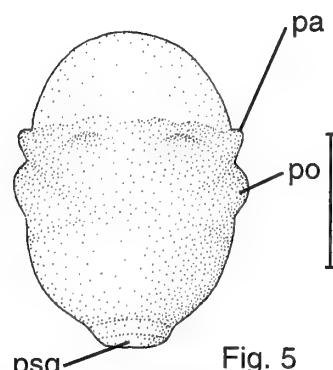
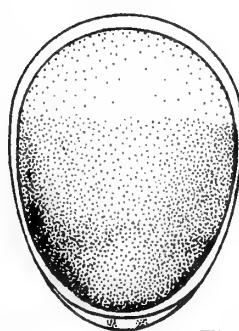
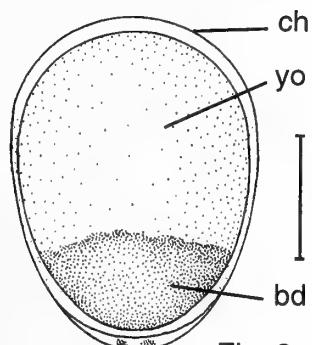
DISCUSSION

The eggs of *L. gahi* developed rapidly from stage 1 to stage 10 during the first five days after spawning. Formation of the germ layer (gastrulation) is a complex process that begins when the margin of the blastoderm becomes two-layered as described in *L. pealei*, *L. vulgaris*, *L. forbesii*, and *L. bleekeri* (Singley, 1977; Marthy, 1982; Segawa et al., 1988; Hun-Baeg et al., 1992). The definitive separation of the blastoderm into an ectodermal and a mesodermal germ layer is accomplished during stages 12 and 13 (III). Thereafter, the developmental pattern of the eggs became linear with a gentle slope (Figure 2). This developmental pattern in *L. gahi* was similar to that observed in *L. pealei* and *L. bleekeri* (Arnold, 1965; Hun-Baeg et al., 1992). However, Segawa et al. (1988) found a sigmoid curve in the internal organogenesis of *L. forbesii*.

As shown in Table 2, at a similar range of temperature, the average development time and mantle lengths of loliginid hatchlings seem to be inversely related to the egg size. Furthermore, egg diameter in other species ranges in size from 1.0–3.3 mm. Therefore, *L. gahi* has relatively large eggs (2.5–3.2 mm). Hatchlings of *L. gahi* are of medium size. They are smaller than *L. bleekeri* and *L. forbesii* and larger than *L. pealei* (Table 2). Same species-specific differences may exist in the first appearance of the organs. At present, the embryonic development using living embryos is suitable for comparison of six *Loligo* species (*L. gahi*, *L. aff. gahi*, *L. bleekeri*, *L. pealei*, *L. vulgaris reynaudii*, and *L. forbesii*). Naef (1928) described the embryological development of *L. vulgaris*, but based on preserved embryos instead of living animals. Fields (1965) described the embryological development of *L. opalescens*, but related the development to daily growth rather than to a staging system that could be applied over a range of temperatures and development rates.

The pattern of chronological appearance of organs is quite similar in the loliginid species examined so far. However, several differences are evident among these species (Figure 15). The primordium of the shell gland (PSG) appears in *L. bleekeri*, *L. aff. gahi*, and *L. gahi*

Figures 3 to 14. Ventral view of embryonic development of *Loligo gahi*, from stage 13 of Arnold (1965) to newly hatched squid. See Results for details of each figure. Key to abbreviations: aliys, anterior lobe inner of the yolk sac; ap, anal papilla or flaps; bd, blastoderm; bh, brachial heart; bu, buccal mass; ch, chorion; f, funnel; g, gill; ho, Hoyle's organ; is, ink sac; m, mantle; o, optic vesicle; pa, primordia of arms; paf, primordia of anterior funnel fold; pf, primordia of fins; pg, primordia of gill; pl, primordia of lens; pliys, posterior lobes inner of the yolk sac; pm, primordia of mantle; po, primordia of optic vesicle; ppf, primordia of posterior funnel fold; ps, primordia of suckers; psg, primordia of shell gland; pst, primordia of statocysts; r, retina; sg, shell gland; st, statocysts; su, sucker; yo, yolk. Scale bar: 1 mm.



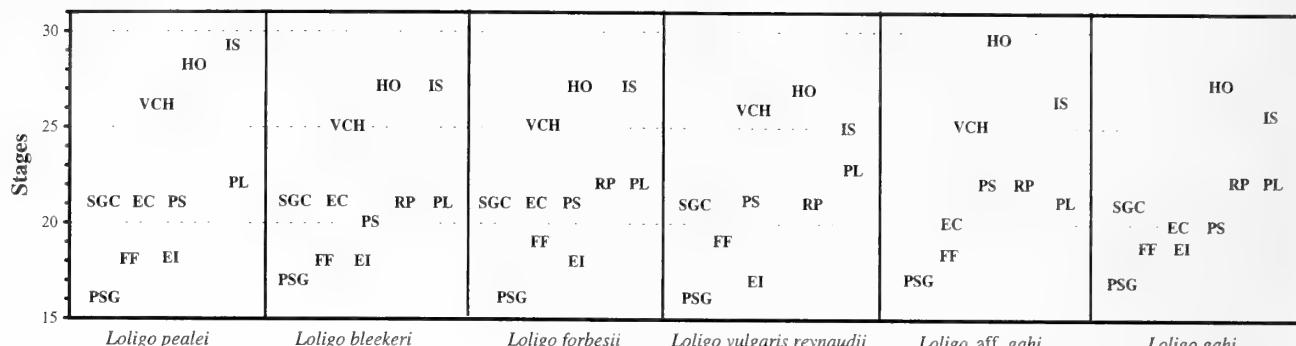


Figure 15. Comparison of chronological appearance of select organs in six species of the genus *Loligo*, using Arnold's (1965) stage system. Key to abbreviations: EC, eye vesicle closed; EI, eye vesicle invagination begins; FF, funnel formation begins; HO, Hoyle's organ appears; IS, ink sac appears; PL, primordia of lens visible; PS, primordia of suckers appear; PSG, primordia of shell gland appears; RP, retina pigmentation begins; SGC, shell gland closed; VCH: ventral mantle chromatophores appear.

later (stage 17) than in *L. vulgaris reynaudii*, *L. pealei*, and *L. forbesii* (stage 16). Funnel formation starts in stage 18 in all loliginid species examined except in *L. vulgaris reynaudii* and in *L. forbesii* (stage 19). Eye vesicle invagination begins to occur in *L. gahi* in stage 19, whereas it occurs in stage 18 in *L. pealei*, *L. bleekeri*, and *L. forbesii*. Barón (1997b) gives no information on when this change occurs in *Loligo* aff. *gahi*. Closure of the eye vesicle occurs in both *L. gahi* and *L. aff. gahi* during stage 20, whereas it occurs during stage 21 in the other species. Appearance of the primordia of suckers (PS) on the tentacles was observed in stage 20 for *Loligo gahi* and *L. bleekeri*, and in stage 21 for *L. pealei* and *L. forbesii*. Barón (1997a) and Blackburn et al. (1998) observed the appearance of primordia of suckers in stage 22 in *L. aff. gahi* and *L. vulgaris reynaudii*, respectively. Retina pigmentation appears in *L. gahi* later (stage 22) than in the other loliginid species. This, however, could be due to the lack of suitable observations in these species as was the case with the primordium of lens. Ink sac (IS) appearance occurred in *L. gahi* and *L. aff. gahi* earlier (stage 26) than in the other three species previously analyzed (stages 27–29), except in *L. vulgaris reynaudii* where it occurred in stage 25. Hoyle's organ (HO) was observed in *L. gahi*, *L. vulgaris reynaudii*, *L. forbesii*, and *L. bleekeri* in stage 27, but it occurs in stage 29 in *L. pealei*. Barón (1997b) indicated that this form is visible in stage 29–30. In all cases, differences among species were restricted within a narrow range of no more than three stages. All of the above-mentioned differences might be due to different observation techniques or rearing conditions (temperature, oxygen concentration, salinity, etc.) rather than heterochronies, as discussed by Boletzky (1987). Although all congeneric species we compared our results with were studied using living embryos, not all of them were maintained under the same conditions.

The chromatophore pattern and size of newly hatched *L. gahi* were quite similar to that observed in *L. aff. gahi* and *Loligo* sp. (Barón, 1997a; 1998).

Brakoniecki (1986) placed all of the American *Loligo* species (e.g., *L. gahi*, *L. opalescens*, *L. pealei*, and *L. plei*) in a separate genus, *Doryteuthis* Naef, 1912, because of several distinct morphological characteristics of the hectocotylus. This author considered that *L. bleekeri* and *L. pealei*, placed by Natsukari (1984) within the genus *Heteroteuthis*, could be a junior synonym of *Doryteuthis*. Comparison of organogenesis of *Doryteuthis* and *L. forbesii* revealed no differences between these species. Similar linear curves of internal organogenesis have been observed in all *Doryteuthis* species. However, these curves are different from the sigmoid curve found by Segawa et al. (1988) in the organogenesis of *L. forbesii*.

Hunter & Simon (1975) previously reported on the extreme homogeneity observed in the morphological development of loliginid squids. Indeed, this homogeneity does not allow one to determine whether the embryonic development described by Barón (1997b) belongs to *L. gahi*, although the similarity of the chromatophore pattern in newly hatched specimens suggests that both might be the same species. However, further comparative studies are necessary to elucidate this issue.

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Gastropoda and Monoplacophora from Hydrothermal Vents and Seeps; New Taxa and Records

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Abstract. A monoplacophoran species and about 100 species of gastropods are recorded from hydrothermal vents and various kinds of seeps from the Atlantic and Pacific Oceans. Previously described species are supplemented with new information on distribution, ecology, morphology, and systematics. The zoogeography of these faunas is discussed and it is noticed that there is a good resemblance in generic composition between the vent and seep localities, while the species usually occur in only one of the two environments. More than 95% of the species found in vents have not been found outside this environment, and the endemic species make up more than 99.5% of the individuals. The fauna of the seeps is less well demarcated. Two species of *Provanna* (Caenogastropoda, Provannidae) are recorded from sunken drift wood in the NE Pacific. The genus was previously thought to be endemic to vent and seep environments. The fauna of the recently investigated vent system at the East Pacific Rise, 17°S is very similar to that of the more northern (9–21°N) localities; 14 species out of 16 are shared. Available evidence for a hypothesized relict character of the gastropod fauna is evaluated and failed to support the hypothesis. Spermatophores were found in *Melanodrymia* sp., the first known case in Neomphalina. A possible case of imposex is reported from the conid genus *Phymorhynchus*. The first monoplacophoran from hydrothermal vents is described, *Rokopella segonzaci*, sp. nov. (Family Neopilinidae), from the Mid-Atlantic Ridge at about 38°N. The following new gastropod taxa are described. Patellogastropoda. Family Neolepetopsidae: *Paralepetopsis ferrugivora*, sp. nov., from the Mid-Atlantic Ridge, 37°N; *P. lepichoni*, sp. nov., from the Nankai Trough off south-eastern Honshu, Japan. Vetigastropoda. Family uncertain: *Adeuomphalus trochanter*, sp. nov., from the Juan de Fuca Ridge; *Sahlingia xandaros*, gen. et sp. nov., from the Aleutian Trench. Family Lepetodrilidae: *Lepetodrilus atlanticus*, sp. nov., from the Mid Atlantic Ridge, 23–38°N. Family Sutilizonidae: *Sutilizona pterodon*, sp. nov., from the Mid-Atlantic Ridge, 23°N; *S. tunnicliffae*, sp. nov., from the Juan de Fuca Ridge. Skeneidae: *Bruceiella athlia*, sp. nov., from seeps in the Aleutian Trench. Trochidae: *Falsimargarita nauduri*, sp. nov., from vents at the East Pacific Rise at 17°S; *Fucaria mystax*, sp. nov., from vents off eastern New Guinea. Uncertain position. Family Neomphalidae: *Melanodrymia galeronae*, sp. nov., from the East Pacific Rise at 13°N; *Retiskenea diploura*, gen. et sp. nov., from the Aleutian Trench; *Lacunoides vitreus*, sp. nov., from the Juan de Fuca Ridge. Family Peltospiridae: *Lirapex costellata*, sp. nov., from the Mid-Atlantic Ridge at 37°N; *Nodopelta rignea*, sp. nov., from the East Pacific Rise at 13°N; *Peltospira smaragdina*, sp. nov., from the Mid-Atlantic Ridge, 15–38°N. *Depressigyratatura* Goedert & Benham, 1999, from Eocene seep deposits in the state of Washington is transferred to *Retiskenea*. Neritimorpha. Family Phenacolepadidae: *Shinkailepas briandi*, sp. nov., from the Mid-Atlantic Ridge, 15–38°N. Caenogastropoda. Family Cerithiopsidae: *Speculator cariosus*, gen. et sp. nov. from the Juan de Fuca Ridge. Family Vitrinellidae: *Neusas*, gen. nov., *marshalli* (Sykes, 1925), from the bathyal Northeast Atlantic. Family Elachisiniidae: *Laeviphitus desbruyeresi*, sp. nov., from the Mid-Atlantic Ridge, 37°N. Buccinidae: *Bayerius peruvianus*, sp. nov., from seeps off Peru; *Eosipho auzendei*, sp. nov., from vents at the East Pacific Rise at 17°S. Conidae: *Bathybela papracea*, sp. nov., from Gulf of California, off Jalisco; *Phymorhynchus major*, sp. nov., from the East Pacific Rise at 13°N; *P. carinatus*, sp. nov., from the Mid-Atlantic Ridge, 15–23°N; *P. ovatus*, sp. nov., from the Mid-Atlantic Ridge, 15–37°N. Heterobranchia. Family Hyalogyrinidae: *Hyalogyrina globularis*, sp. nov., from the Juan de Fuca Ridge; *H. umbellifera*, sp. nov., from seeps in the Aleutian Trench. Family Orbitestellidae: *Lurifax vitreus*, gen. et sp. nov., from the Mid-Atlantic Ridge, 37–38°N. Family Xylodisculidae: *Xylodiscula analoga*, sp. nov., from the Mid-Atlantic Ridge, 37°N.

INTRODUCTION

The importance of chemosynthetically nourished environments in the sea is becoming more and more obvious. These environments include many biotopes, from a normal sea bottom with an inflow of organic material higher than the available oxygen can oxidize, to hydrothermal vents. In the latter, sulfides or other oxidizable compounds are released from deeper sediments or rocks where they have been trapped as minerals, via phreatic water. When the outflow is slow, especially when there are no defined outlets for the water, usually the term seep or seepage is used. Among the compounds used by the bacteria are, in addition to sulfides, methane, reduced iron, and manganese compounds.

High concentrations of sulfides, hydrocarbons, and heavy metals are toxic for most animals. These biotopes may therefore become isolated, and most areas around hydrothermal vents harbor a specialized fauna (Carney, 1994; Fustec et al., 1987; Grassle, 1986b; Hessler & Lonsdale, 1991a, b; Hessler, 1985; Hessler & Smithey, 1983; Tunnicliffe, 1988, 1991; Hessler & Kaharl, 1995). When the availability of oxidizable compounds is high, the biomass and number of individuals may become very high, but the number of species is low (Grassle, 1986b, 1989).

We here report on previously unstudied collections of Gastropoda (and two specimens of Monoplacophora) made by several investigators and research organizations in various vent and seep environments.

MATERIALS AND METHODS

The present study is based mainly on the French (IFREMER/DRO/EP) explorations of the hydrothermal activity at the East Pacific Rise [hereafter EPR] and the Mid-Atlantic Ridge [hereafter MAR]. We have, however, also included material from other localities, vents and seeps, when such has been available. All localities are listed in Appendix 1, where also references to further information on the biotopes and expeditions are given. Material collected by French (IFREMER) expeditions is deposited in MNHN. No museum number is allocated to individual lots, but the material reported in this paper is unambiguously designated (and retrievable) through the combination of expedition acronym, e.g., MARVEL, and station/dive number, e.g., dive 1195. This information is present on labels accompanying individual lots.

The specimens on which our work is based are listed under each species. They are there listed according to locality (north to south), by expedition and a reference number to the sampling. More detailed position data are given in Appendix 1. Unless otherwise stated, the material is stored in Muséum national d'Histoire naturelle.

Much of the French material was found after dives in the "retrieval box" ("panier"), which means that the specimens were gathered there during the dive, without

detailed notes on their origin. They can, however, be localized to the area where the dive was made and constitute important material for variation, abundance, and anatomical investigation.

As usual with material from "general" samplings, the fixation is highly variable. Gastropods need to be individually anesthetized to allow the fixative quick access to the soft parts. When preserved in bulk mixed with bottom material, the results are highly variable. Occasional specimens may be good, especially such where the shell has been damaged. Nevertheless, one can usually find specimens good enough to allow an informative picture of the external morphology. Such specimens have been used for critical-point drying, via 99.5% alcohol and carbon dioxide. For anesthetization of gastropods we recommend isotonic magnesium chloride ($MgCl_2 \times 10H_2O$, 72.3 gram per liter of fresh water). This is slowly added to the jar with seawater where the crawling specimens are kept, during 10 minutes to a few hours and in small portions. When they do not react to touch, try transferring the least important specimen to the fixative. Different species may take different times to get ready for fixation.

Patellogastropod radulae (see McLean, 1990a) as well as those of chitons (Macey et al., 1997) and to some extent those of Monoplacophora (Warén & Gofas, 1997), contrary to most other gastropod radulae, are sensitive to treatment with strong potassium hydroxide, which usually is employed to clean the organ from the surrounding tissues (Figures 2a, d). After tests with various concentrations and times, we have instead macerated the radular sac or small specimens in 0.5% KOH at 40–50°C for 10–20 hours. This causes no damage, but much organic material remains. The radulae were then cleaned in diluted commercial bleach (3 parts water: 1 part bleach) for a short time (1–30 seconds depending on size), carefully rinsed in distilled water, and mounted on histological cover slips. For large radulae we used a thin layer of carefully dried polyvinyl acetate glue to make them stick better to the substrate. Comparison with the most anterior part of the same radula, from the buccal cavity, which had been dissected out, showed no destruction (Figures 2b, e, g).

In descriptions and figures of radulae, we have numbered the teeth sequentially, counting the central tooth as "0," the first lateral tooth "1," etc.

ABBREVIATIONS

CENTOB	Centre de Tri d'Océanographie Biologique, Brest
EPR	East Pacific Rise
FMNH	Field Museum of Natural History, Chicago
IFREMER	
DRO/EP	Institut Français de Recherches pour l'Exploitation de la Mer/Direction de la Re-

	cherche Océanographique/ Département Environnement Profond
JdF	Juan de Fuca Ridge system, from southern Juan de Fuca to Explorer Ridge
LACM	Los Angeles County Museum of Natural History, Los Angeles
MAR	Mid-Atlantic Ridge
PL	Plongée (dive)
MNHN	Muséum national d'Histoire naturelle, Paris
SMF	Senckenbergisches Museum und Forschungsinstitut, Frankfurt
SMNH	Swedish Museum of Natural History, Stockholm
sh(s)	shell(s) with no soft parts
spm(s)	live taken specimen(s)
TVG	TV monitored grab, 1.82 m ²
TVGKG	TV monitored box corer
USNM	National Museum of Natural History, Washington, D.C.
WP	West Pacific vent systems

DESCRIPTIONS AND SYSTEMATIC LIST OF NEW SPECIES AND RECORDS

Class MONOPLACOPHORA

Family NEOPILINIDAE Knight & Yochelson, 1958

Rokopella Starobogatov & Moskalev, 1987

Rokopella Starobogatov & Moskalev, 1987:10.

Type species: *Neopilina oligotropha* Rokop, 1972; by original designation; north of Hawaii, abyssal.

Remarks: Warén & Gofas (1997) reviewed the small species of Monoplacophora with reticulate sculpture and recognized *Rokopella* and *Veleropilina* Starobogatov & Moskalev, 1987, as distinct genera, with three and five species, respectively. They summarized the distinctive features, and we refer to there for further information.

We have classified the new species described below in *Rokopella* because its sculpture is very similar to other species of the genus; the foot and gills are very small; and the pallial furrow is very broad and shallow. The arrangement of the perioral ridges and tentacles agrees as far as the poor preservation allows comparison. *Rokopella segonzaci* does, however, differ in having the apex situated well outside the margin of the shell, and in having three pairs of gills only (Haszprunar, personal communication).

The apical area of the two specimens is badly corroded, but there seems not to be a pitted zone around the "apical cap" as in *Veleropilina*; instead the first sculpture to appear is the network of concentric and radial ribs, as in other species of *Rokopella*.

Rokopella segonzaci Warén & Bouchet, sp. nov. (Figures 1a–e)

Type material: Holotype and 1 paratype in MNHN.

Type locality: MAR, Menez Gwen: DIVA 2 PL 11, 37°50.54'N, 31°31.30'W, 860–870 m, on shells of *Bathymodiolus* sp.

Material examined: Only known from the type material.

Distribution: Only known from the type locality.

Etymology: Named after Michel Segonzac at IFREMER, who has supervised the sorting of all material collected by French expeditions from hydrothermal vents.

Description: Shell (Figures 1d–e). Very small and flat for the group, transparent, fragile, with well visible sculpture and thick periostracum. The apical area is corroded in both specimens, but the sculpture starts already at a diameter of 0.1 mm. The apical cap forms an angle of about 30° with the basal plane of the shell. Only traces remain of the first sculpture but very soon it develops into a slightly irregular network of equally strong radial and concentric ribs. These ribs are slightly irregular and make little jerks and twists at the intersections, but do not form tubercles. The shell is covered by a thick and tough periostracum, but this was peeling in both specimens, and only traces remained at the first examination. The ratio length/breadth is 1.38, height/length is 0.29.

Dimensions. Maximum diameter of holotype 0.90 mm; paratype 0.82 mm.

Soft parts (Figure 1c). The foot is small and circular, its diameter corresponds to 0.22 of the length of the shell in critical-point dried specimens. The pallial furrow is wide and shallow; its width corresponds to a little less than half the diameter of the foot. There are three small, simple, fingerlike, and inconspicuous gills, of which the posterior one is twice as large as the others. They seem to lack ciliation, except a longitudinal strip along the anterior-inner side, but this may be an artifact of poor preservation. They are all strongly wrinkled transversally and seemingly capable of considerable elongation. In a broken gill two large longitudinal vessels can be seen. The perioral organs are low and inconspicuous; the anterior lip consists of a simple semicircular ridge. The vela are hardly connected in front of the lip; they are attached for the anterior third of their length; the posterior two-thirds is a simple skinfold. The posterior lip is a low and inconspicuous ridge. The posterior tentacle ridge is interrupted in the center; laterally there is a lappet, but no tentacles.

Radula (Figures 1a, b). Normal for the family, long and slender with 11 teeth per transverse row. Tooth number 0 has a strong denticle at each side of the main cusp. Teeth 1–3 are of similar size and shape with three-four, five, and four strong cusps, respectively. Tooth 4 has ca. 22 cusps. Tooth 5 has the usual scooplike appearance.

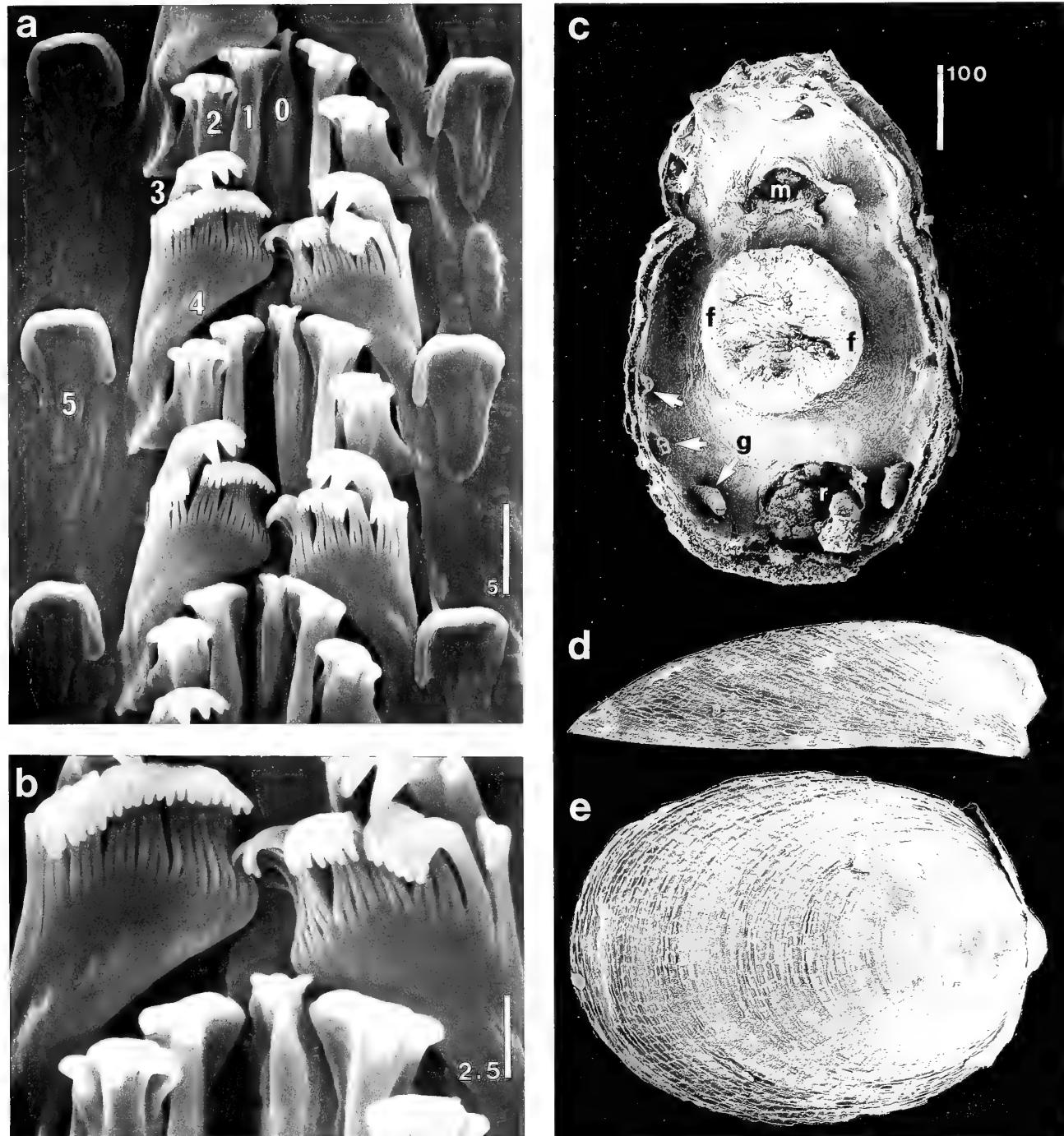


Figure 1. *Rokopella segonzaci* Warén & Bouchet, sp. nov. a, b. Radula. Numbers indicate sequential order of teeth with central tooth as 0. c. Ventral view of soft parts, body wall broken at anus. d, e. Shell of holotype, maximum diameter 0.90 mm. f - foot; g - gill; m - mouth; r - rupture of pallial roof. Scale bars in μm .

Remarks: The start of the sculpture at a diameter of only 0.1 mm indicates that the sculpture starts immediately after the apical cap, as in *R. euglypta* (Dautzenberg & Fischer, 1896), although in that (larger) species the cor-

responding diameter is 0.2 mm. The low profile of the shell may indicate that the specimens are juveniles; this is, however, contradicted by the sculpture being more crowded toward the edge.

Rokopella segonzaci differs from *R. euglypta* by being proportionally more elongate (L/B 1.38; 1.15 in *R. euglypta*) and by having fewer and coarser cusps on radular teeth 0–3 (five, 13, seven, and eight in *R. euglypta*).

The low number of gills, only three, is a difference from *Rokopella oligotropha* and *R. euglypta*, which have five pairs. This is probably connected with the small size, since *Micropilina minuta* Warén, 1989, which is also of a similar size, has only three pairs of gills.

This is the first monoplacophoran to be found at modern hydrothermal vents, but since it was found only once, we are not sure that *R. segonzaci* is a regular member of the vent fauna, although its habitat, on shells of *Bathymodiolus* may support this view. The species may also have been overlooked because of its small size. There are three additional species of Monoplacophora known from nearby parts of the Mid-Atlantic Ridge (Warén & Gofas, 1997).

Class GASTROPODA

We have largely followed the arrangement of the gastropods proposed by Ponder & Lindberg (1997). For the reader not mainly interested in gastropod taxonomy, it can be mentioned that the old concept Archaeogastropoda corresponds to Patellogastropoda plus Vetigastropoda plus Cocculiniformia plus Neritimorpha. "Caenogastropoda" corresponds to the old concepts "Mesogastropoda" plus "Neogastropoda," and "Heterobranchia" corresponds to "Opistobranchia" plus "Pulmonata".

Subclass PATELLOGASTROPODA

Family NEOLEPETOPSIDAE McLean, 1990

Remarks: McLean (1990a) discussed deviations in radular characters compared with other Patellogastropoda and concluded that "Lepetopsina" (a "suborder" proposed for some fossils and the docoglossate limpets from hydrothermal vents) is a less modified group within the "Patellogastropoda" (= Docoglossa). Fretter (1990) described the anatomy of several species and believed the group to be more closely related to the Acmaeidae than to the Patellidae, which contradicts a position as a discrete "suborder" of the Patellogastropoda. McLean's (1990a) conclusions about the distinctness of the Lepetopsina were mainly based on the radular characters of the Recent species, and since we will here show that those characters are partly based on misinterpretations, we con-

sider that Lepetopsina needs a more thorough reevaluation, beyond the intentions of the present report. For preparation of neolepetopsid and docoglossate radulae, see "Materials and Methods."

We have noticed a variation in radular development among the vent limpets (*Paralepetopsis*, *Neolepetopsis*, and *Eulepetopsis*). Some species are more similar to true limpets (*Patella*, etc.) in the development of mineralized cusps of the teeth. Examples of this are *Neolepetopsis densata* (Figure 2a), *N. gordensis* (Figure 2d), and *Paralepetopsis ferrugivora* (Figures 2e–f). They have defined apical cusps, although we have not investigated the presence of iron compounds. Other species like *Paralepetopsis lepichoni* (Figure 2c) and *Eulepetopsis vitrea* (Figures 2b, g) do not develop apical cusps. This difference, however, does not necessarily mean very much systematically since it corresponds to the maturation of the teeth along the radula. In *P. ferrugivora*, for example, about half the length of the radula, including the part in use, has well developed cusps (Figure 2e). Along the recently formed part, the teeth lack strengthened cusps (Figure 2f), and are very similar to those that never develop them. In this state they are also similar to the teeth of young, non-vent limpets (Patellidae and Lepetidae examined). Therefore we simply consider the radular differences from non-vent limpets a result of heterochrony.

Neolepetopsid limpets usually live on rocks and shells, more rarely vestimentiferan tubes. The gut is usually filled with reddish brown, granular masses. This seems to come from the ferruginous crusts, which cover large parts of the hard substrates in the vents. These crusts harbor a fauna in which we noticed nematodes and ciliates to be common. Together with the bacteria that precipitate the iron oxides and hydroxides, these organisms seem to form the main food.

Neolepetopsis McLean, 1990

Neolepetopsis McLean, 1990a:492.

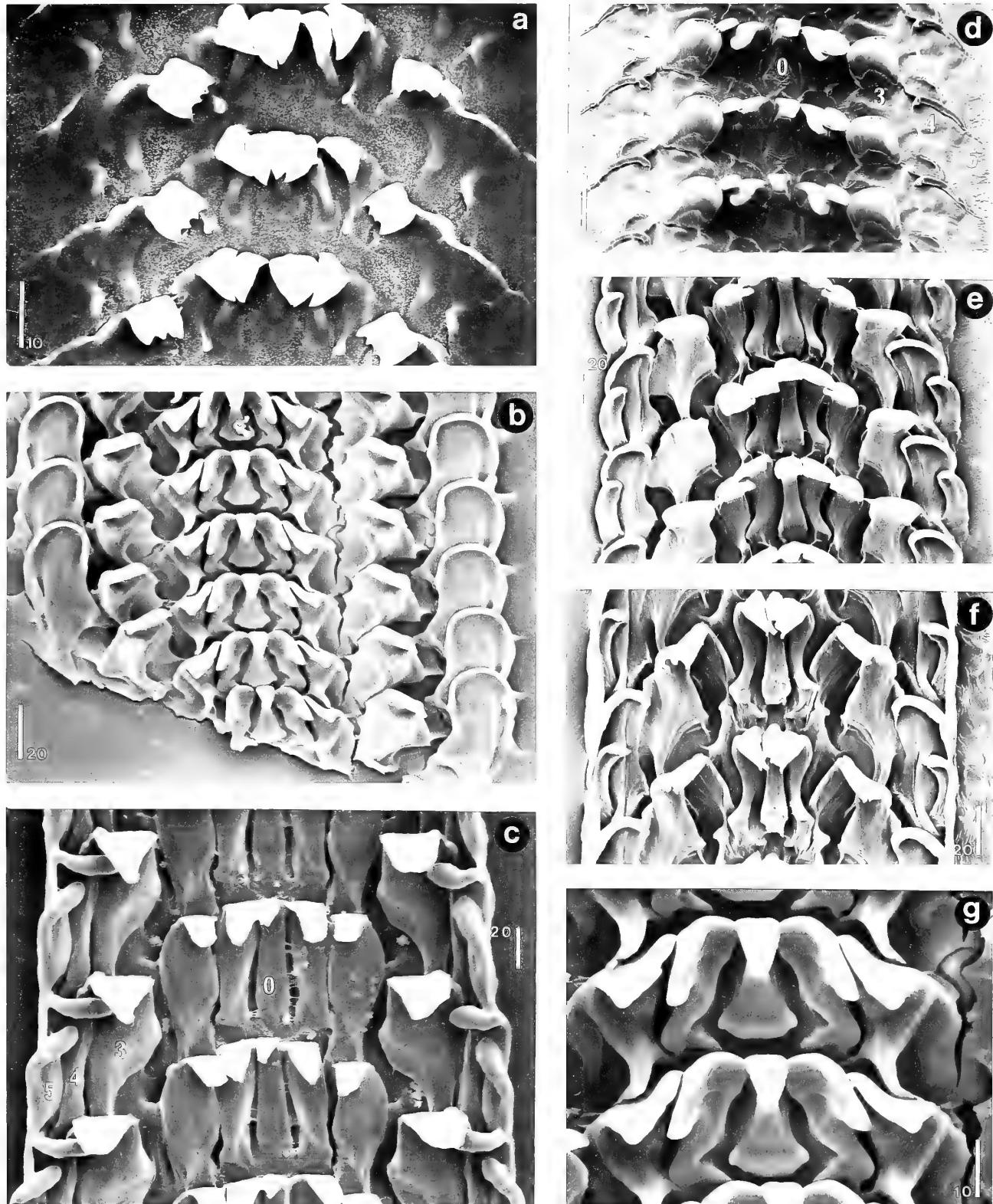
Type species: *N. gordensis* McLean, 1990; by original designation; Gorda Ridge, off northern California.

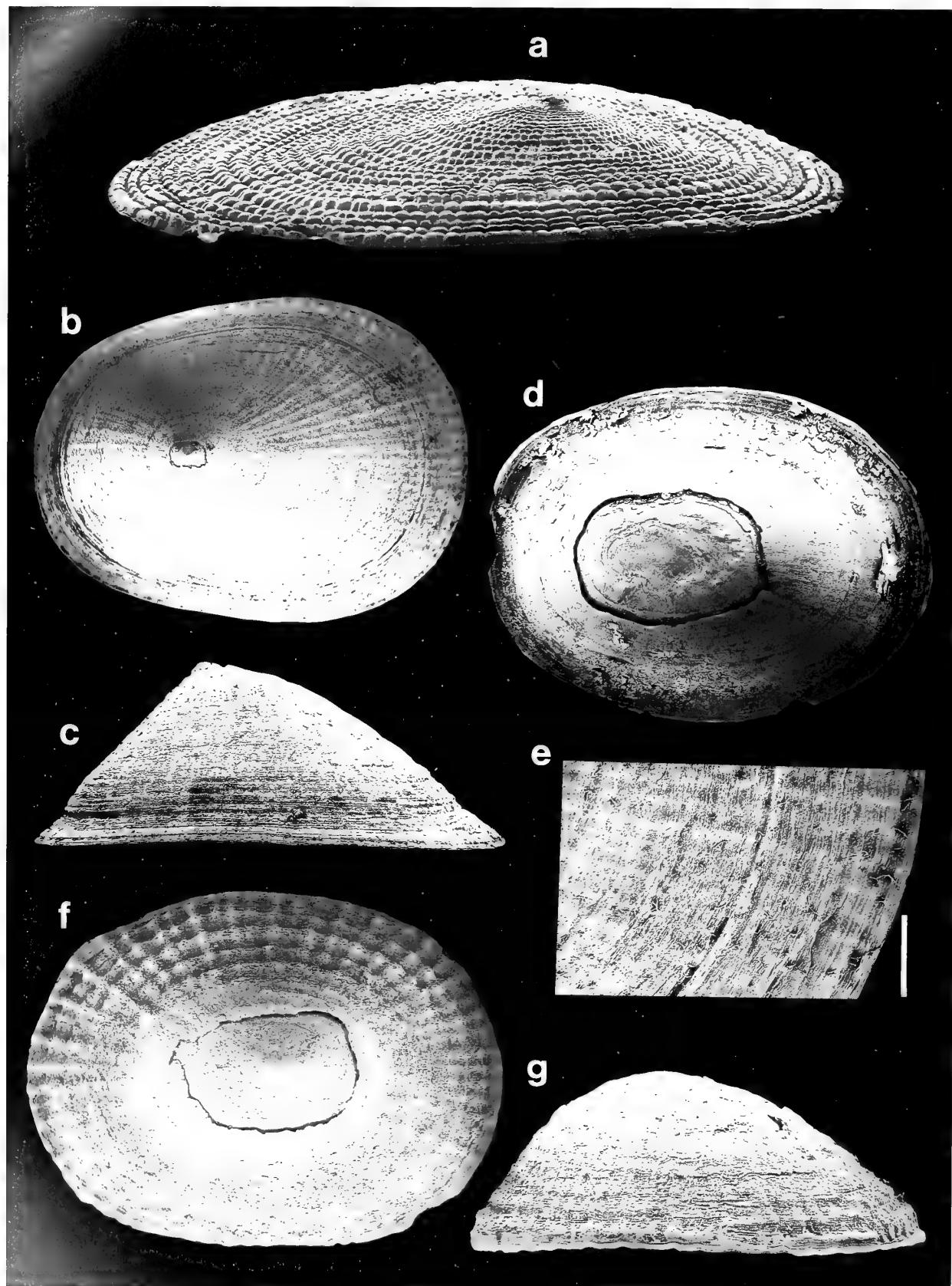
Neolepetopsis cf. gordensis McLean, 1990

(Figures 2d, 3f–g)

Neolepetopsis gordensis McLean, 1990a: 492, figs. Ia–h, IIa–g.

Figure 2. Neolepetopsidae, radulae. Numbers indicate sequential order of teeth with central tooth as 0. a. *Neolepetopsis densata*, EPR at 13°N. Partly damaged by KOH b, g. *Eulepetopsis vitrea*, EPR at 13°N, whole width and detail of central field. c. *Paralepetopsis lepichoni* Warén & Bouchet, sp. nov., holotype, old part. d. *Neolepetopsis gordensis*, Jalisco Block Seeps. e, f. *Paralepetopsis ferrugivora* Warén & Bouchet, sp. nov., MAR, Lucky Strike. e. Old part, treated with bleach (apical cusp broken off the center left pluricuspidate tooth). f. Newly formed part of radula. Scale bars in μm .





Neolepetopsis sp.: Warén & Bouchet, 1993:88 (fauna list only).

New records: *Mid America Trench, Jalisco Block Seeps at 20°N*: - NAUTIMATE PL 10, 10 shs, 2 spms; - NAUTIMATE PL 16, 2 spms, on rocks. *Off Peru*: - NAUTI-PERC PL01-4-13, 3 spms.

Distribution: From the Gorda Ridge, 41°00.4'N, 127°29.3'W, ca. 3200 m and south of Gulf of California, 20°01.79'N, 106°17.33'W, 3795 m, south to off Peru, 05°S, ca. 3500 m.

Remarks: Whether the three specimens from off Peru belong to *N. gordensis*, or not, is uncertain. McLean's material indicated high variability, the species is very featureless, all specimens are corroded, and our Peruvian specimens were found far away from the type locality. The records may belong to the same species, but our identification should, by no means, be used as an indication of faunal affinity between the localities.

We figure the shell (Figures 3f-g) and radula (Figure 2d) of specimens from the Jalisco Block Seeps, which are most probably conspecific with *N. gordensis*.

Neolepetopsis densata McLean, 1990

(Figures 2a, 3a, 15a-c)

Neolepetopsis densata McLean, 1990a: 496, figs. IIIa-g, IVa-d.

New records: *EPR at 13°N*: - HERO 91 PL 11, 1 spm; - HERO 91 PL 25, 13 spms; - HERO 92 dive 2522, 1 spm.

Distribution: Galapagos Rift (Gustafson & Lutz, 1994) and EPR at 13°N in 2630 m and 11°46'N, 103°47'W, 2725 m (from an inactive sulfide chimney).

Remarks: Our specimens agree closely with McLean's description and we feel confident in the identification. The species is characteristic with a very flat, transparent shell and small wart-shaped apex. We figure the protoconch (Figures 15a-c) which was damaged in McLean's specimens, and an adult shell (Figure 3a). Figure 2a shows a partly destroyed radula, but the shape of the cusps agrees with that shown by McLean (1990a).

Eulepetopsis McLean, 1990

Eulepetopsis McLean, 1990a:503.

Type species: *E. vitrea* McLean, 1990; by original designation; hydrothermal vents at EPR, 21°N.

Remarks: The genus *Eulepetopsis* remains monotypic.

Eulepetopsis vitrea McLean, 1990

(Figures 2b, g; 14c)

Eulepetopsis vitrea McLean, 1990a:503, figs VIIa-I, VIIIa-j, IXa-f.

New records: *EPR at 13°N*: - HERO 91 PL 12, 3 spms; - HERO 92 dive 2516, 1 spm; - dive 2517, 10 spms; - dive 2519, 1 spm; - dive 2523, 1 spm; - dive 2528, 12 spms. *EPR at 09°50'N*: - HERO 91 PL 07, 4 spms. *EPR at 17°S*: - NAUDUR PL 06, site Rehu, 27 spms; - NAUDUR PL18.4.8b, site Rehu, 2 spms.

Distribution. EPR from 21°N to 17°S, and the Galapagos Rift, in 2450–2630 m depth.

Remarks: We figure the radula and jaw (Figures 2b, g; 14c) since McLean's (1990a: fig. IX) preparations were somewhat damaged by KOH. The gut is usually filled with ferruginous deposits.

Paralepetopsis McLean, 1990

Paralepetopsis McLean, 1990a:510.

Type species: *P. floridensis* McLean, 1990; by original designation; sulfide seeps at the Florida Escarpment.

Remarks: The differences between *Neolepetopsis* and *Paralepetopsis* are not very distinct. *Neolepetopsis densata*, *occulta*, and *verruca* all have a fairly similar, flat and partly transparent shell, while *N. gordensis*, the type species of *Neolepetopsis*, has a taller, opaque shell very similar to *Paralepetopsis floridensis*, the type species of *Paralepetopsis*. The radulae are not known in enough detail to allow comparison.

Paralepetopsis ferrugivora Warén & Bouchet, sp. nov.

(Figures 2e-f; 3b-e; 4a-b, e; 14a-b)

Type material: Holotype and one paratype in MNHN.

Type locality: MAR, Lucky Strike, 37°17.50'N, 32°17'W, 1665–1728 m.

Material examined: MAR, Lucky Strike: - DIVA 1 PL 17, 2 spms; - DIVA 1 PL 19, 2 spms; - DIVA 2 PL 03, 1 spm; - DIVA 2 PL 05, 1 sh; - DIVA 2 PL 09, suction sample among mussels and hydrothermal sediments, 1 spm; DIVA 2 PL 10, on a rock, 1 spm; retrieval box, 11 spms; - DIVA 2 PL 19, 1 spm; - ALVIN dive 2608 (Tour Eiffel), 1 spm; - LUSTRE Exp. (Tour Eiffel), on mussels, 1 spm; - MARVEL PL1194 (Tour Eiffel), retrieval box, 2 spms.

Figure 3. Neolepetopsidae, shells. a. *Neolepetopsis densata*, EPR at 13°N, 8.1 mm maximum diameter b-e. *Paralepetopsis ferrugivora* Warén & Bouchet, sp. nov. b, c, e. Holotype, 8.0 mm diameter. e. Detail of sculpture, scale bar 0.5 mm. d. Large corroded specimen, 9.4 mm. f, g. *Neolepetopsis gordensis*, Jalisco Block Seeps, maximum diameter 4.9 and 4.3 mm.

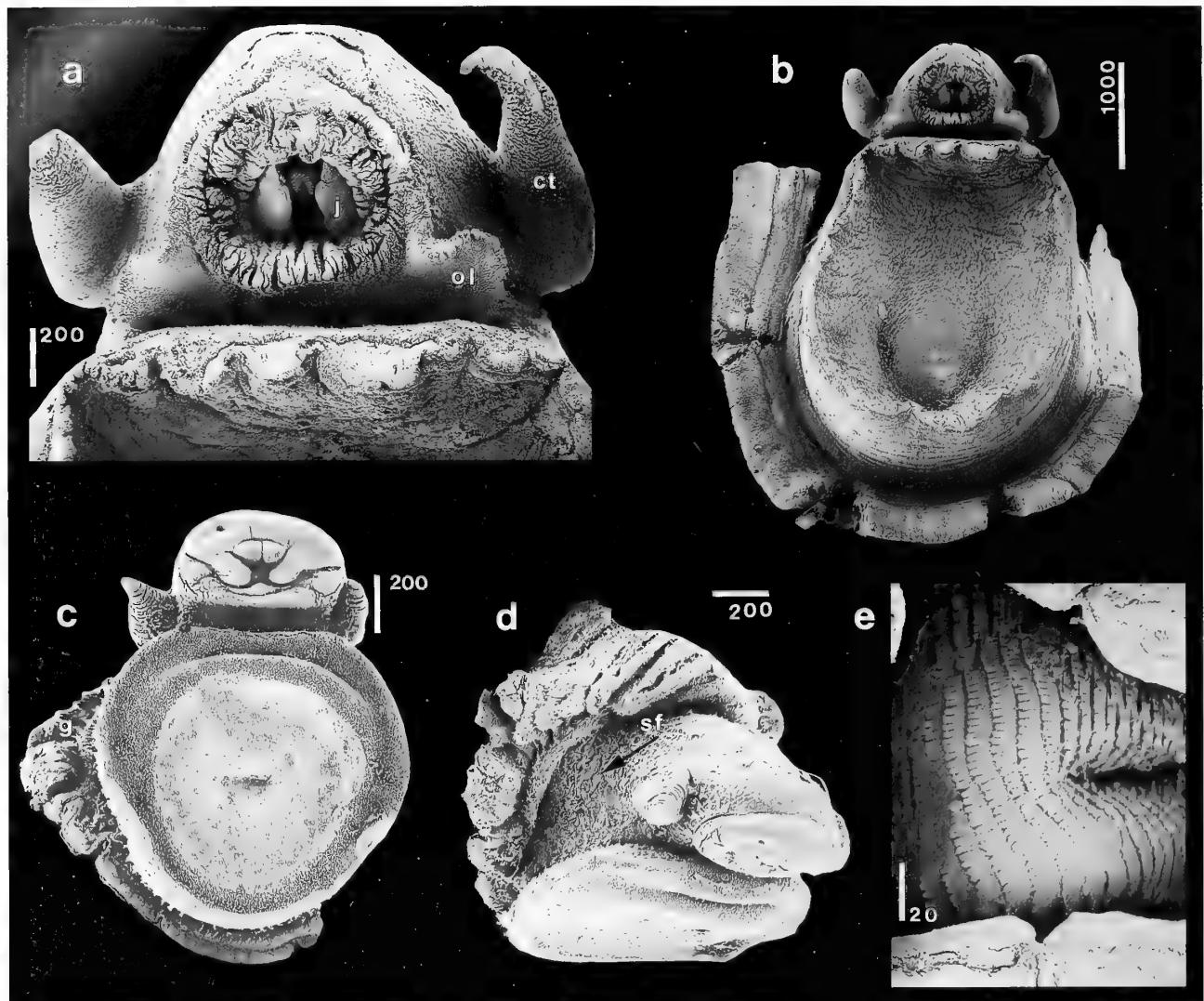


Figure 4. *a, b, e.* *Paralepetopsis ferrugivora* Warén & Bouchet, sp. nov., soft parts. *a.* Anterior part of head-foot *b.* Body, ventral view, anterior part of pallial skirt removed. *e.* Detail of licker. *c, d.* *Pyropelta corymba*, Oregon Margin. *c.* Ventral view of head-foot. *d.* Anterolateral view to show gill, pallial skirt folded backward. *ct* - cephalic tentacle; *g* - gill; *ol* - oral lappet; *sf* - seminal furrow. Scale bars in μm .

Distribution: Only known from the Mid-Atlantic Ridge at Lucky Strike, about 1700 m depth.

Etymology: From “ferrugo” and “voro,” Latin, meaning rust and to eat.

Description: *Shell* (Figures 3b–e). Of normal size for the genus, sturdy, depressed, and with a rough surface. Juvenile specimens and the protoconch are not known. The apex is situated at the anterior $\frac{1}{3}$ and worn in all specimens we have seen. The anterior surface of the shell is straight in profile, the posterior one weakly convex. The periostracum is thin and colorless, hardly noticeable. The outer layer of the shell is semitransparent, slightly brownish or colorless, and rough. A thick medium layer is per-

fectly transparent, giving an impression of “empty space.” It is followed by an inner, white, chalky and thin layer with concentric pattern, which easily peels off. The sculpture consists of numerous radial ribs.

Dimensions. Maximum diameter of holotype 8.0 mm, height 2.7 mm, maximum diameter seen, 9.2 mm.

Soft parts (Figures 4a, b, e). The external morphology agrees well with the original description of the genus and Fretter's (1990) more detailed account. It can be added that the licker (*sensu* Fretter 1990:532) has transverse, regularly crenulate folds all over its surface (Figure 4e).

Radula (Figures 2e–f). The part in use and half the length backward has well developed and strengthened cusps on the central tooth and the three inner teeth at

each side (Figure 2e). The more recently formed part lacks reinforcement and its teeth are soft (Figure 2f). The central tooth has a simple, straight cutting edge like a chisel and a more slender shaft which basally is flattened and carries a small antero-lateral ridge at each side. The first lateral tooth is of similar shape, is slightly broader, and has a single lateral, more sturdy and curved lateral ridge. The second lateral resembles the first, but the base is tapering and the basal ridge central, and forms an articulation toward the center. The third lateral tooth ("pluricuspid tooth") has a cutting edge twice as broad as number 2, is larger and more sturdy, and its cutting edge has two to three low and blunt tubercles. Its base is broad, and the centrally placed ridge is drawn out anteriorly. The two outer teeth are simple and scooplike; the outer one is half the size of the inner one.

Remarks: *Paralepetopsis ferrugivora* differs from *P. floridensis* in having square instead of triangular cusps on the central and lateral radular teeth, by having more distinct radial sculpture on the shell, and by lacking papillae on the pallial margin. There are two different color forms of *P. ferrugivora*: the shell is either white or slightly orange-brown, but we have seen no intermediate variations.

The intestine is always full of orange-brown matter with a granular structure with many nematode and ciliate fragments. This seems to be the bacterially precipitated "rust deposit" of most hard surfaces that are scratched off together with its inhabitants.

Paralepetopsis lepichoni Warén & Bouchet, sp. nov.

(Figures 2c, 5a–f)

Type material: Holotype in MNHN.

Type locality: Off south-eastern Honshu, Nankai Trench seeps, KAIKO-NANKAI 14, 33°49.40'N, 137°55.20'E, 2140 m.

Material examined: Only known from the holotype.

Distribution: Only known from the type locality.

Etymology: Named after Xavier Le Pichon, leader of the expedition that retrieved the specimen.

Description: *Shell* (Figures 5a–f). Greyish white, slightly discolored by very thin, brown ferruginous deposits, rather thick and sturdy, ovate, depressed, with anteriorly situated apex. The protoconch is not known. The anterior surface is straight; the posterior one distinctly convex. The shell is sculptured by numerous, fine and sharp radiating with small scalelike tubercles (Figures 5b, d).

Dimensions. Maximum diameter of holotype 9.8 mm, height 2.8 mm.

Soft parts. Not examined, specimen dried.

Radula (Figure 2c). Apical cusps of teeth not strengthened. The central tooth is slender with a bluntly pointed apical cusp. The first and second lateral tooth are quite similar to each other, the inner one slightly more slender. The third lateral tooth is twice as broad as these and its basal ridge is turned away from the center. The two outer teeth are not well visible in the preparations, but it can be seen that the outer one is considerably smaller.

Remarks: The gut was filled with sediment in the holotype, not ferruginous crusts as is usually the case in the family.

Subclass COCCULINIFORMIA

Family PYROPELTIDAE McLean & Haszprunar, 1987

Pyropelta McLean & Haszprunar, 1987

Pyropelta McLean & Haszprunar, 1987:197.

Type species: *P. musaica* McLean & Haszprunar, 1987; by original designation; hydrothermal vents, JdF

Pyropelta cf. *musaica* McLean & Haszprunar, 1987

(Figures 6a–b, 7c)

Pyropelta musaica McLean & Haszprunar, 1987:198, figs. 1–8, 9A.

Pyropelta musaica: McLean, 1992b:406, figs. 9–16.

New records: JdF, Axial Seamount, Ashes vent field: - ROPOS R406, 5 spms (FMNH 280892). Mid America Trench, Jalisco Block Seeps at 20°N: - NAUTIMATE PL 10, 2 shs; - NAUTIMATE PL 16, on rocks, 4 spms.

Distribution: JdF, Axial Seamount, 1575 m, at vents, and on whale skeletons, several localities off California, 33–36°N, 940–1400 m. Possibly also south to the Jalisco Block Seeps at 20°N, 3000–3775 m.

Remarks: The radula of one of the specimens from the Jalisco Block seeps (Figure 7c) was compared with McLean & Haszprunar (1987) and McLean's (1992b) illustrations and no differences were found. All specimens of "this species," ours and McLean's, have lost the primary shell surface by corrosion (Figures 6a, b), and we find it impossible to be certain that they belong to the same species.

Pyropelta corymba McLean & Haszprunar, 1987

(Figures 4c–d, 6c–f, 7a–b)

Pyropelta corymba McLean & Haszprunar, 1987:200, figs. 9–11.

Pyropelta corymba: McLean, 1992b:409, figs. 17–24.

New records: Oregon Margin: - ROPOS #339, Pete Vent

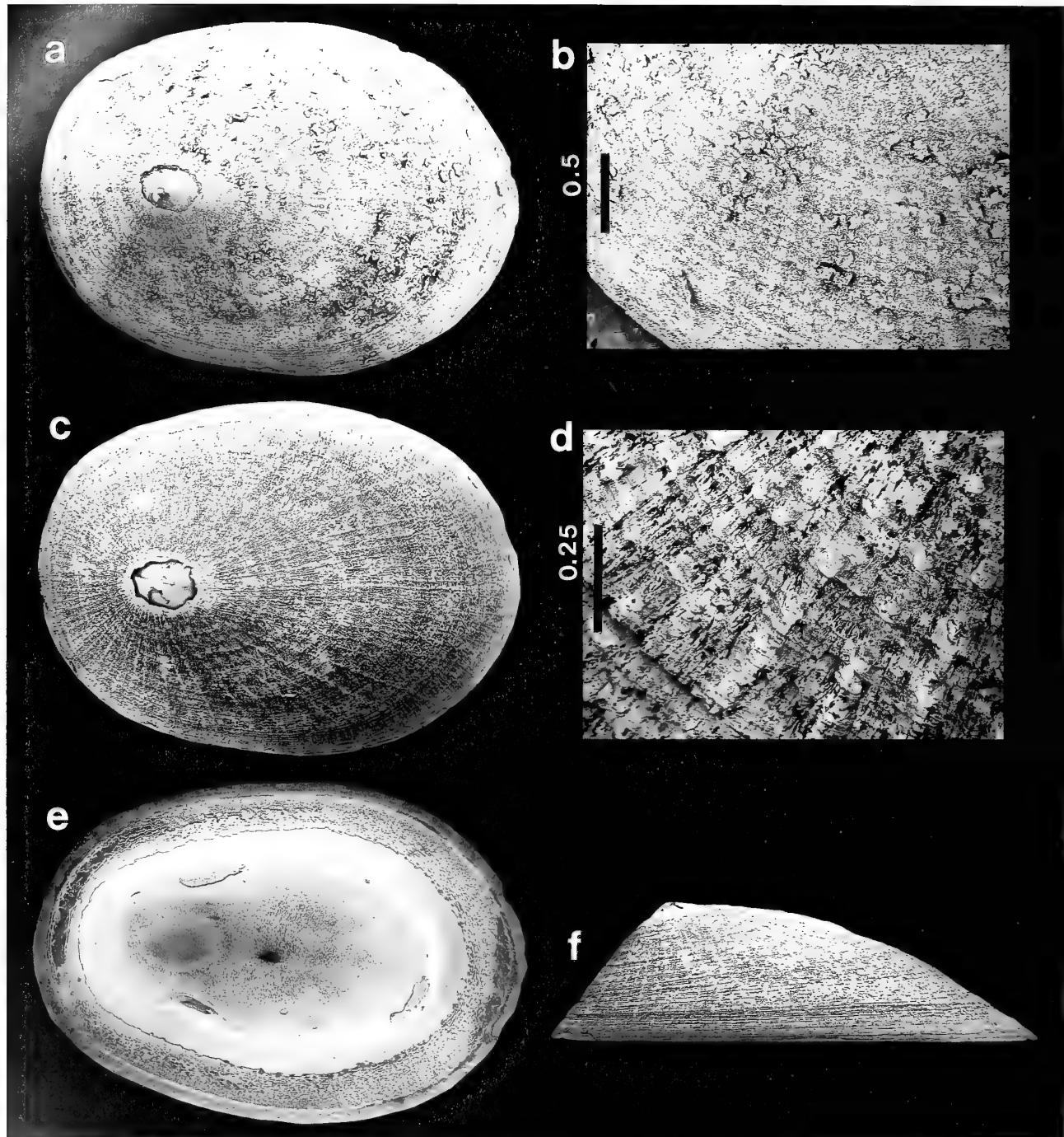


Figure 5. *Paralepetopsis lepichoni* Warén & Bouchet, sp. nov., holotype, maximum diameter 9.8 mm. *a*, *b*. Shell *c*, *d*. Shell cleaned with bleach. *e*. Inside of shell. *f*. Lateral view.

Field, 3 spms on shell of live *Provanna laevis* (SMF 311990); - TVG 11, 1 spm on shell of live *Provanna laevis*.

Distribution: Hydrothermal seeps in the Guaymas Basin

to seeps at the Oregon Margin, 2022–524 m, also on whale bone (McLean, 1992b).

Remarks: We figure a critical-point dried specimen, shell and radula to facilitate future identification. The differ-

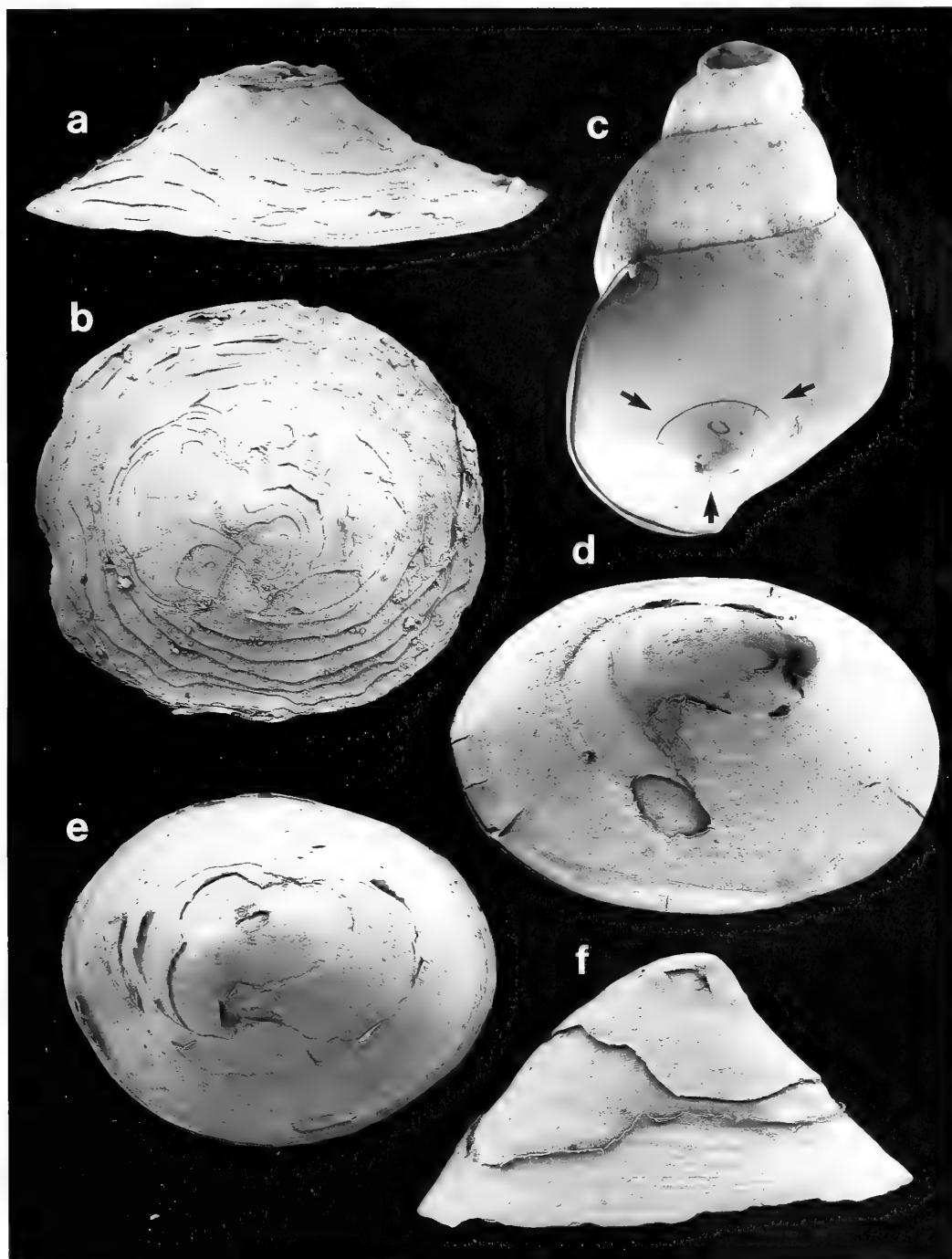
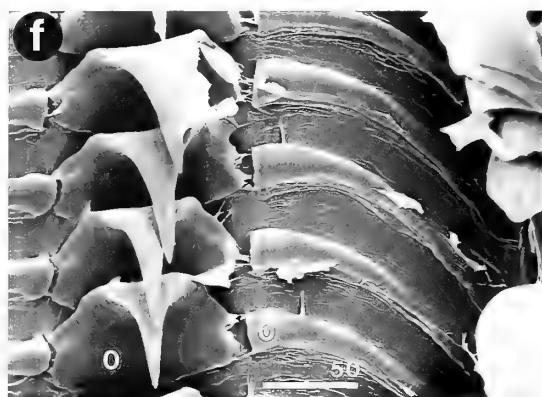
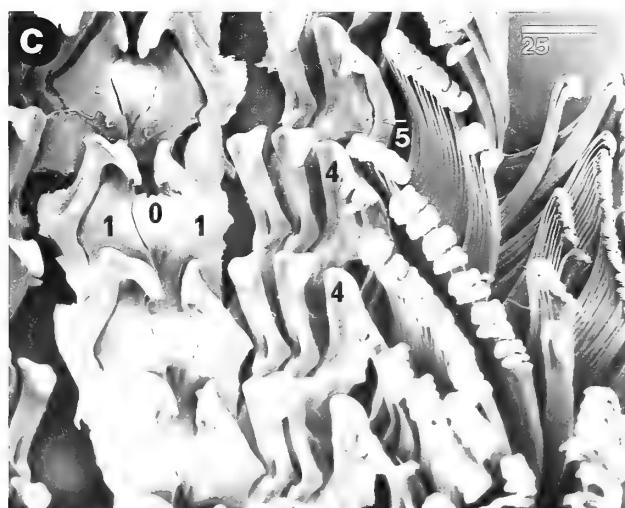
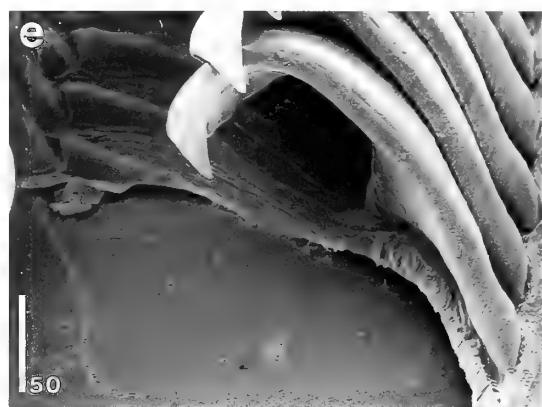
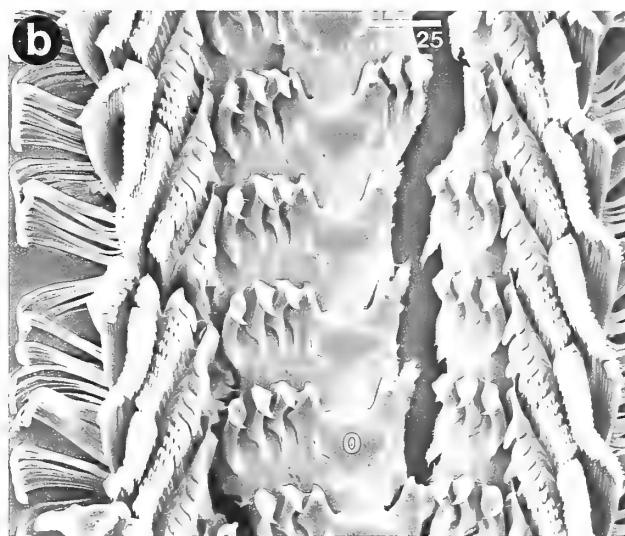
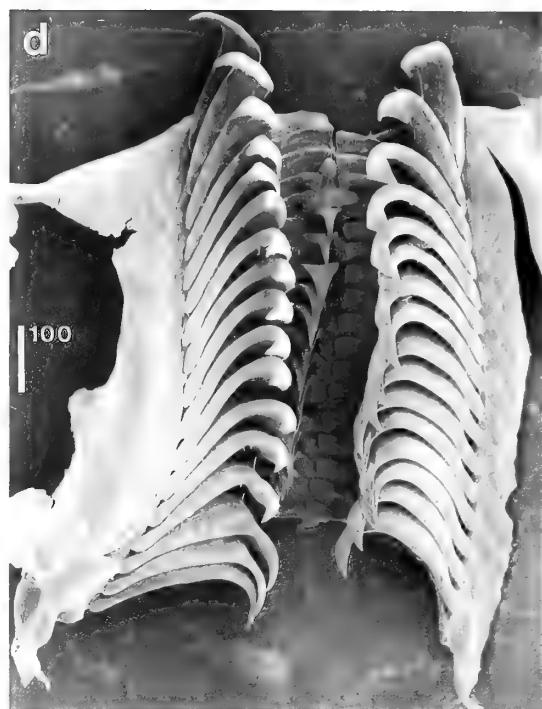
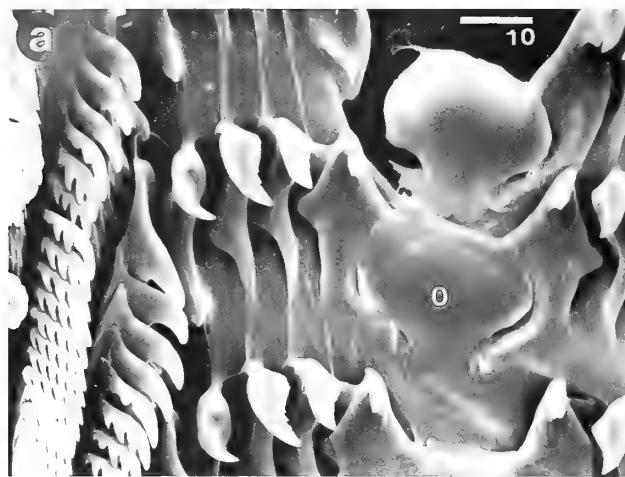


Figure 6. *Pyropelta* spp., shells. a, b. *P. cf. musaica*, Jalisco Block Seeps. a. Lateral view, maximum diameter 3.4 mm. b. Apical view, maximum diameter 4.6 mm. c-f. *P. corymba*, Oregon Margin. c. In situ, diameter 1.9 mm, on a living specimen of *Provanna laevis*. d. Same specimen removed. e, f. Adult specimens, diameter 2.8 and 2.5 mm.

ence between the three known species of *Pyropelta*, consists mainly of the much flatter shell of *P. musaica* and *P. craigsmithi* (McLean, 1992) and we do not know if there may be additional species hidden. The radula of *P.*

corymba differs considerably from *P. musaica* in having strong denticles on the lateral and inner marginal teeth.

McLean (1992b) completed the original description with several figures of the radula. We do believe there is



a good possibility that our identification is correct since *P. corymba* was described from the same seep system as *Provanna laevis*, and our present records indicate an association between the two species.

The shell muscle is semicircular, anteriorly broader, its left side has an indistinct "hook." The gill is restricted to the right part of the pallial cavity and enters the right pallial furrow. There is a conspicuous seminal furrow from the right part of the pallial cavity to the right cephalic tentacle.

Subclass VETIGASTROPODA

Family Uncertain

Sahlingia Warén & Bouchet, gen. nov.

Type species: *Sahlingia xandaros*, sp. nov.

Diagnosis: "Vetigastropods" with a small to medium size, simple, fragile shell with slightly curved incremental lines. Pallial cavity unusually deep, with single, monoplectinate left gill far over to right side. Cephalic tentacles triangular, short, and flat with unusually long sensory papillae along sides. Eye-lobe and eye absent. Right neck-lobe triangular; left one absent. A single epipodial tentacle under operculum. Radula 1 - 1 - 1; radular sac bilobed. Rhachidian tooth extremely low and broad, with single cusp and small triangular central body. "Marginal teeth" hooklike with simple, sturdy, and flattened base.

Etymology: Named after Heiko Sahling, Kiel, who collected the type species.

Remarks: *Sahlingia* is still one more example of a vetigastropod that can not easily be placed in a family level or higher taxon. The position in the Vetigastropoda is supported by the presence of sensory papillae and bilobed radular sac, but the external morphology of the soft parts and shell is too simple and plesiomorphic to allow inferences. The radula is too simplified and specialized to be of any use except its presence and as a synapomorphy of the members of the genus.

We have earlier encountered two undescribed species, in normal deep-sea environment, which can be classified in *Sahlingia*. One was found at 2000 m depth at the Lord Howe Rise (between Australia and New Zealand), the other from 4000 m depth in the Bay of Biscay, each represented by a single specimen. They both have conspicuously yellow soft parts. The radula was prepared of the one from the Bay of Biscay and proved to differ only by having the cusps of the "marginal" teeth finely serrated.

It seems quite probable that *Thalassonerita eocenica* Squires & Goedert, 1996, described from Middle-Eocene cold-seeps in the Humptulips Formation in Washington, belongs to this new genus. The size, shape, and sculpture are similar, but no protoconchs are known. It was described in Neritidae (?), but its shell is thin and has an umbilicus which is contradictory to a position in Neritidae.

Sahlingia xandaros Warén & Bouchet, sp. nov.

(Figures 7d-f, 8a-b, 9a-d, 15d, 16h)

Type material: Holotype SMF311980 and 1 paratype SMF311981, 1 paratype SMNH5082, 1 paratype (TVG 43) in MNHN.

Type locality: Aleutian Trench Seeps, Edge site, TVGKG 24, 57°27.394'N, 148°00.013'W, 4890 m - 3 spms.

Material examined: The types and: *Aleutian Trench*: - TVG 43, 2 spms.

Distribution: Only known from the material above. Aleutian Trench Seeps at about 4800–4900 m depth.

Etymology: From "xandaros" (Greek), clear, distinct; from its deviating appearance.

Description: *Shell* (Figures 8a, b). Of medium size, rounded with depressed spire, colorless, with very thin brownish transparent periostracum and deep umbilicus. The protoconch (Figure 15d) is pale brownish and has slightly more than half a whorl, diameter 390 µm; the sculpture is not known (covered by deposits that had corroded its surface). The teleoconch has up to 2.7 whorls of rapidly increasing diameter and is sculptured with numerous sharp, incremental lines, and scattered, very indistinct spiral lines. In addition to the incremental lines, there are also a few axial lines that differ in curvature and probably represent longer periods of absence of growth. The outer lip is thin and fragile, not noticeably thickened, and very slightly expanded. The umbilicus is not surrounded by a keel and there are no ribs on the reflected inner lip. The peristome is large, more tangential than radial, prosocline, almost round, slightly indented by the preceding whorl. The outer lip is shallowly sinuated at the mid-point of its height.

Dimensions. Diameter of holotype, 5.6 mm, maximum diameter 9.7 mm.

←
Figure 7. Radulae. Numbers indicate sequential order of teeth with central tooth as 0. a,b. *Pyropelta corymba*, Oregon Margin. a. Detail of central part. b. Whole width. c. *P. cf. musaica*, Jalisco Block Seeps. d-f. *Sahlingia xandaros* Warén & Bouchet, gen. & sp. nov., Aleutian Seeps, Edge site. d. Half the length of the radula. e. Detail of central part showing the basal part of the lateral tooth. f. Central teeth. Scale bars in µm.

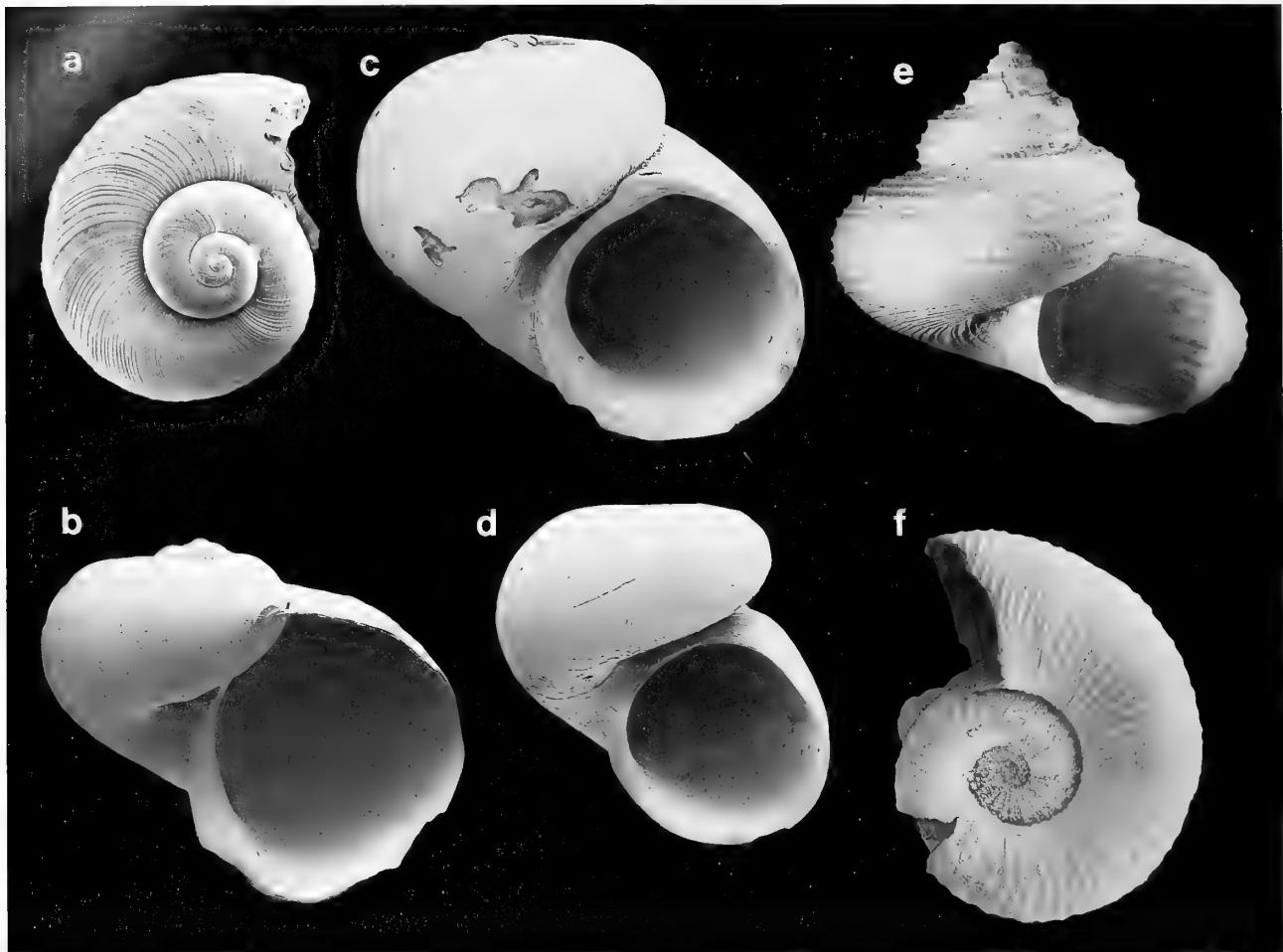


Figure 8. Shells. *a,b.* *Sahlingia xandaros* Warén & Bouchet, gen. & sp. nov. *a.* Paratype, apical view, diameter 5.8 mm. *b.* Holotype, diameter 5.6 mm. *c.* *Fucaria mystax* Warén & Bouchet, sp. nov., apical whorls lost, Aleutian Seeps, Shumagin site, diameter 2.4 mm. *e.* *Falsimargarita nauduri* Warén & Bouchet, sp. nov., holotype, height 18.6 mm. *f.* *Adeuomphalus trochanter* Warén & Bouchet, sp. nov., holotype, diameter 2.7 mm.

Soft parts (Figures 9a-d). The milky white soft parts are retracted only very shallowly into the shell and seem not to be able to withdraw farther. The pallial cavity reaches almost one whorl backward, and the monopectinate gill can be seen by transparency along the right(!) side of pallial cavity. It is very long, ca. 40 leaflets, of mainly even width, corresponding to $\frac{1}{3}$ of the width of the pallial cavity. There is a conspicuous efferent axis along its left side. The leaflets are tall, and bursicles are probably not present. The foot is large, flat, posteriorly rounded, anteriorly drawn out to unusually long lateral corner tentacles. There is one little, wartlike epipodial "tentacle" under the anterior part of operculum. At the ventral, left side of the neck, a small "wart" (a sensory papilla?) is connected to the corresponding epipodial tentacle by an indistinct ridge. At the right side of the neck is a flat tentacle, below and partly covered by the cephalic tentacle, perhaps a neck-lobe derivative. The snout is long

and broad with the triangular, unusually flat cephalic tentacles attached far back. Eyes are absent. The sides of the cephalic tentacles are richly equipped with sensory papillae.

Operculum (Figure 16h). Transparent, yellowish at the zone of attachment, multispiral with central nucleus and short growth zone.

Radula (Figures 7d-f). 1 - 1 - 1, short and broad with ca. 39 transverse rows. The central tooth is very low and broad with a triangular central part and a long lateral process at each side. The point of the central triangle is curved backward and free from secondary denticles. The lateral processes are broken both in the standard preparation and in a specimen which was critical-point dried with everted buccal mass. The lateral tooth is flattened, claw-shaped, with a simple apical cusp. Before being dried, the radula was bluish violet. The radular sac is bilobed at its posterior end.

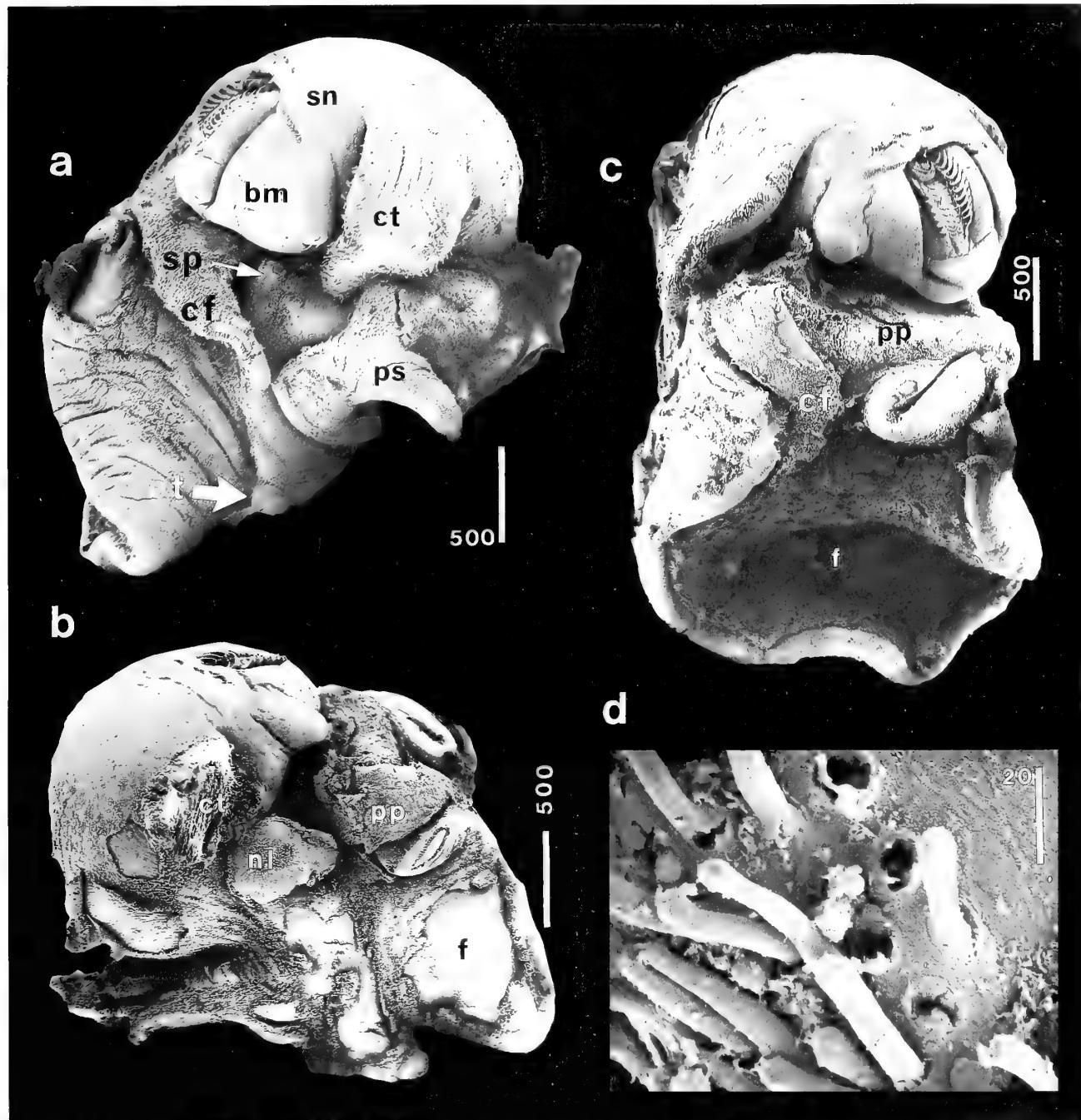


Figure 9. *Sahlingia xandaros* Warén & Bouchet, gen. & sp. nov., critical-point dried. *a*. Head-foot, left side. *b*. Head-foot, right side. *c*. Head-foot, front view. *d*. Detail of sensory papillae from cephalic tentacle. bm - buccal mass; cf - corner of foot; ct - cephalic tentacle; et - epipodial tentacle; nl - neck-lobe; pp - propodium; ps - pallial skirt; sn - snout; sp - sensory papilla. Scale bars in μm .

Remarks: We are not aware of any species that invite confusion; *S. xandaros* is unusually large for being a “skeneimorph” and is more likely to be confused with a specimen of the capulid genus *Torellia* Jeffreys, 1867 (Neotaenioglossa).

Adeuomphalus Seguenza, 1876

Adeuomphalus Seguenza, 1876:10.

Type species: *A. ammoniformis* Seguenza, 1876; by monotypy; Plio-Pleistocene deep water fossil, southern Italy.

Remarks: The genus was discussed by Warén (1991:74), who pointed out the similarity to *Eudaronia* Cotton, 1945, a vetigastropod genus of uncertain position, from deep water off South Australia. Warén has afterward examined a couple of species of *Adeuomphalus* which turned out to lack a radula, among them, the type species. This lack of a radula was confirmed also in the new species described here, but serial sectioning of the paratype confirmed that it is a vetigastropod, by the presence of sensory papillae on the cephalic tentacles.

Adeuomphalus trochanter Warén & Bouchet,
sp. nov.

(Figures 8f, 151, 16d)

Type material: Holotype (MNHN) and one paratype (SMNH5083), serially sectioned.

Type locality: JdF, CoAxial Segment: Beard Chimney Source site, 46°09.3'N, 129°48.4'W, 2060 m, both specimens found in a running shoe, caught by a grab.

Material examined: Only known from the type material.

Etymology: From “trochanter,” a torture wheel (Latin), referring to the superficial appearance of the shell.

Description: *Shell* (Figure 8f). Small, fragile, colorless, planispiral, with evenly rounded whorls and sigmoid axial riblets. The protoconch (Figure 151) has a diameter of 190 µm, consists of $\frac{1}{3}$ of a whorl, and is sculptured by an irregular net demarcating pits of highly irregular shape and size. The teleoconch is demarcated by a small but distinct rib. The first 1.5 teleoconch whorls are distinctly keeled halfway between the two sutures, at both sides of the shell. Where this keel disappears the axial riblets become slightly flexuous instead of radial and straight. The holotype is slightly broken (the paratype more so), but seems to have had 2.0 whorls. The peristome is circular except for an indentation by the preceding whorl.

Dimensions. Diameter of holotype 2.7 mm, height 1.2 mm; paratype diameter 2.2 mm.

Operculum (Figure 16d). Same diameter as peristome, multispiral with central nucleus, transparent but quite sturdy.

Radula. Absent.

Soft parts. The anterior end of the foot is bifurcated, the corners drawn out to tentacelike formations. The anterior pedal gland is large and conspicuously white in a rehydrated specimen. Epipodial tentacles are present, but no detail could be discerned. The cephalic tentacles are blunt, cylindrical, slightly longer than the large, broad, apically expanded snout, and lack eyes. A right neck-lobe is present; a left one was not detected. The gill is small, monopectinate with 10 leaflets; the outline of the whole gill is semi-circular with the diameter corresponding to the axis and directed straight backward. From what could

be detected by transparency of the soft parts, the visceral mass is mainly occupied by the gonad.

Remarks: Examination of the serial sections confirmed *Adeuomphalus* to be a vetigastropod, but few other details. It is a simultaneous hermaphrodite; its buccal mass, esophagus, and stomach are much simplified and did not contain identifiable material. The gill is monopectinate. The holotype had an arenaceous foram attached to the right side of the shell.

Superfamily TROCHOIDEA Rafinesque, 1815

Family TURBINIDAE Rafinesque, 1815

Cantrainea Jeffreys, 1883

Cantrainea Jeffreys, 1883:109.

Type species: *Turbo peloritanus* Cantraine, 1840; by monotypy; Plio-Pleistocene fossil, Sicily.

Remarks: The type species also occurs living in depths between 100 and 1000 m off southern and western Europe. The genus comprises several bathyal species, worldwide, except in polar areas.

Cantrainea macleani Warén & Bouchet, 1993

Cantrainea macleani Warén & Bouchet, 1993:8, figs. 4A–C, 5B, F–G, 6A.

New records: Off Louisiana: - Johnson Sealink dive 3129, 3 spms (2 with neritid egg capsules on shell).

Distribution: Only known from off Louisiana, Bush Hill Seep, ca. 540 m.

Family TROCHIDAE Rafinesque, 1815

Remarks: We have largely followed Hickman & McLean (1990) in the classification of the family.

Bathymargarites Warén & Bouchet, 1989

Bathymargarites Warén & Bouchet, 1989:87.

Type species: *B. symplector* Warén & Bouchet, 1989; by original designation; hydrothermal vents at the EPR.

Bathymargarites symplector Warén & Bouchet, 1989

Bathymargarites symplector Warén & Bouchet, 1989:91, figs. 92–95, 100–101, 104–107, 110.

Bathymargarites symplector: Warén & Bouchet, 1993:11, figs. 10A–E, 11A–B.

New records: EPR at 13°N: - HERO 91 PL 09, 11 spms; - HERO 91 PL 11 (Genesis), 20 spms; - HERO 91 PL 12, 1 spm; - HERO 91 PL 14 (Elsa), 2 spms; - HERO 92 dive 2520, 1 sh. 09°50'N: - HERO 91 PL 07, 2 spms; - HERO 91 PL 08, 1 spm; - HERO 91 PL 09, 2 spms.

17°S: - NAUDUR PL 06, 34 spms; - NAUDUR PL 18, 5 spms.

Distribution: EPR from 21°N to 17°S. Depth range 2500–2600 m.

Remarks: The new records enlarge the distribution considerably.

Cataegis McLean & Quinn, 1987

Cataegis McLean & Quinn, 1987:113.

Type species: *C. toretuta* McLean & Quinn, 1987 [31 July] (= *Homalopoma finkli* Petuch, 1987 [not dated, hence deemed to be 31 December]); by original designation; deep water off Colombia.

Cataegis meroglypta McLean & Quinn, 1987

Cataegis meroglypta McLean & Quinn, 1987:115, figs. 3, 4, 7, 8.

Cataegis meroglypta: Warén & Bouchet, 1993:19, figs. 14A–G, 15A–B.

New records: Off Louisiana: - Johnson Sealink dive 3129, 35 spms. Off Barbados (El Pilar Sector): - DIAP-ISUB 15-4, 11 spms; - DIAPISUB 16-3, 11 spms.

Distribution: Off Louisiana and Barbados, 540–1135 m.

Remarks: Several specimens from the Bush Hill Seep had the shell tunneled by polychaetes of the subfamily Polydorinae, in one case so wide a tunnel that both the in- and outside of the shell had been broken through. Usually the tubes were restricted to the umbilicus of the shell.

Falsimargarita Powell, 1951

Falsimargarita Powell, 1951:93.

Type species: *Margarites gemma* Smith, 1915; by original designation; Antarctic, bathyal.

Remarks: The genus *Falsimargarita* comprises a few species of mainly Antarctic distribution, in depths between 300 and 3500 m (Dell, 1990:93). We have seen a couple of similar species from deep-sea dredgings around New Caledonia (25°S), but nothing more northern.

The species of *Falsimargarita* have a fragile shell with mainly spiral sculpture. The internal nacreous layer, visible through the surface of the shell, is of a greenish iridescent hue. The protoconch of *Falsimargarita* is finely tuberculate.

The protoconch of species of Calliostomatinae has a diagnostic honey-comb sculpture (Marshall, 1995), but the radula and soft parts are very similar to shallow water species and we consider the placement in Calliostomatinae (Powell, 1951, Marshall, 1995) correct.

Falsimargarita nauduri Warén & Bouchet sp. nov.

(Figures 8e, 10a–d, 11a, b, 14e, 16c)

Type material: Holotype in MNHN.

Type locality: EPR at 17°25'S, NAUDUR PL 04-8-4, site Rehu, 17°24.85'S, 113°12.15'W, 2578 m.

Material examined: The holotype.

Distribution: Only known from the type locality.

Etymology: Named after the expedition that found the species.

Description: *Shell* (Figure 8e). Large, fragile, slightly greenish iridescent, conical with strongly convex whorls. The protoconch is large and inflated, diameter 1.2 mm, with less than half a whorl and almost no suture. Its surface is finely tuberculate. The teleoconch has 4.25 strongly convex whorls. The first whorl is sculptured with three sharp keels, starting directly after the protoconch, of which the adapical one remains close to the suture, the median one becomes number 5, and the abapical one becomes number 8 on the body whorl at the peristome. The total number of major keels at the peristome is 33 plus three recently added minor ones. The axial sculpture starts after ¼ of a whorl, with ribs of similar strength as the spirals, 38 in number on the first ribbed whorl. The axial ribs form tubercles at the intersection with the spines, and on the later whorls they become much less obvious between the spiral ribs, and not much stronger than on the first whorl. The interior of the whorls is covered by a thin nacreous layer and has broad, shallow furrows corresponding to the spiral ribs and low axial ribs reflecting the axial ones of the exterior. Umbilicus deep and narrow.

Dimensions. Height 18.6 mm, diameter 18.7 mm.

Soft parts (Figures 10a–d). The foot is long and slender, laterally covered by small papillae below the epipodial membrane (Figure 10c), smooth above it, posteriorly pointed, anteriorly truncate, slightly bilobed and drawn out to short corner tentacles, paralleled by the propodium. Each side of the foot has an epipodial membrane with smooth dorsal surface and richly covered by papillae similar to those of the sides of the foot but two to three times higher and more pointed, on its ventral side. Halfway backward under the operculum the membrane becomes lower and continues posteriorly as a low papillose ridge. The membrane has six tentacles evenly spaced between the operculum and the neck-lobe. The left neck-lobe starts below the eye-lobe and forms a smooth undulating membrane, continuous with the epipodial membrane. The right neck-lobe is similar, but has a small membrane, drawn out ventrally and entering the right part of the space between the head and foot and connects to the mouth. The

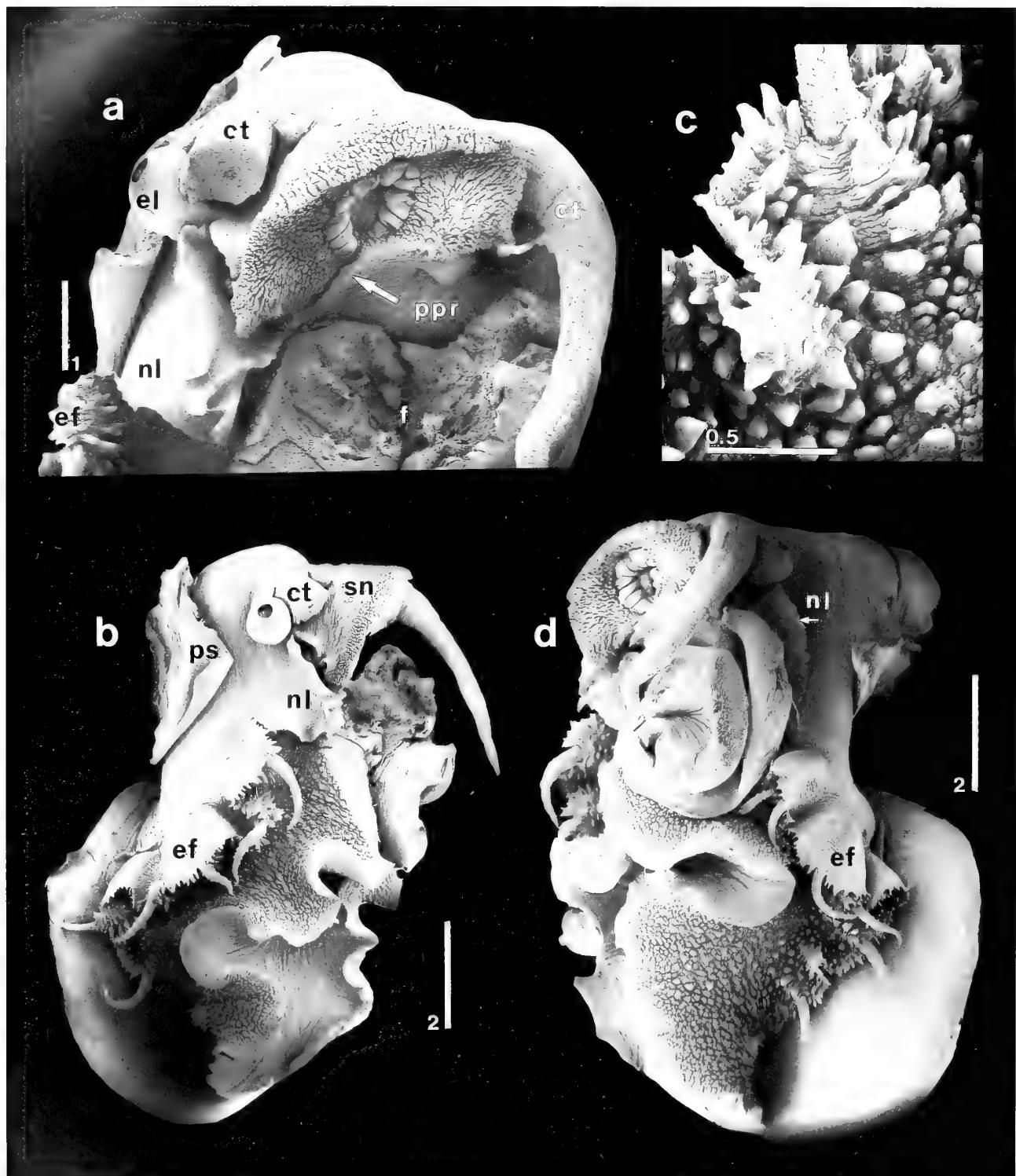


Figure 10. *Falsimargarita nauduri* Warén & Bouchet, sp. nov., holotype, critical-point dried. Right cephalic tentacle and right anterior part of foot removed to show details. *a*. Snout, ventral view. *b*. Head-foot, right side. *c*. Detail of ventral surface of epipodial fringe. *d*. Head-foot, left side. **ct** - cephalic tentacle; **ef** - epipodial fringe; **el** - eye-lobe; **f** - foot (partly cut off); **nl** - neck-lobe; **ppr** - pseudoproboscis; **ps** - pallial skirt; **sn** - snout. Scale bars in mm.

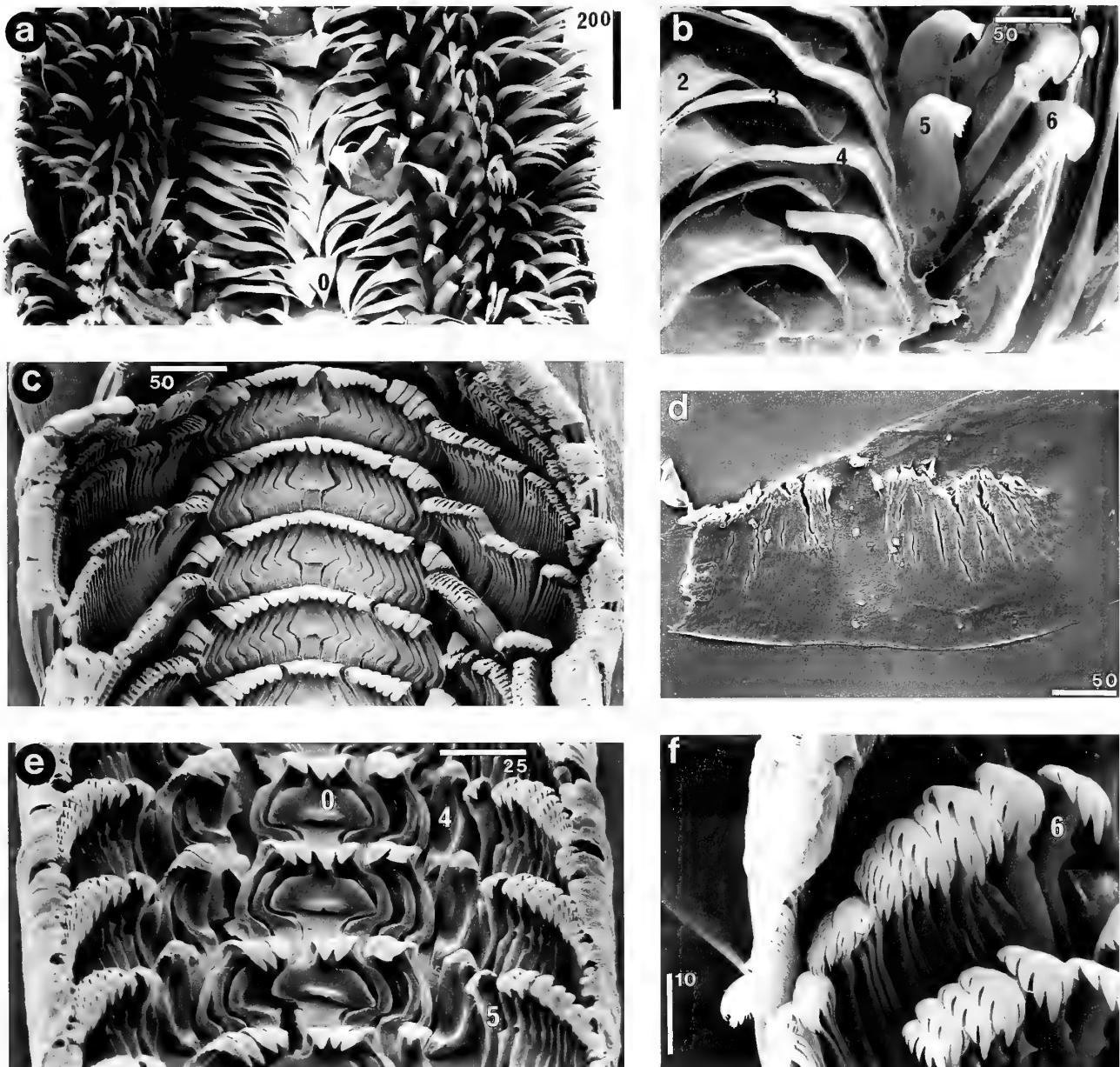


Figure 11. Radulae and jaw. Numbers indicate sequential order of teeth with central tooth as 0. *a*, *b*. *Falsimargarita nauduri* Warén & Bouchet, sp. nov., holotype. *a*. Whole width. *b*. Detail of outermost lateral and innermost marginal teeth. *c*. *Fucaria mystax* Warén & Bouchet, sp. nov., holotype. *d–f*. *Bruceiella athlia* Warén & Bouchet, sp. nov., Aleutian Seeps, Shumagin site. *d*. Jaw. *e*. Whole width of radula. *f*. Detail of marginals.

cephalic tentacles are long and slender with longitudinal furrows. At their anterior, central and basal part is a small cephalic lappet. The eye-lobes are five times as long as the basal diameter and apically inflated to twice the basal diameter, to contain the large, black eye. The snout is short, apically broader, and flattened. Its anterior face is covered by small papillae and sharply demarcated from the oral disc surrounding the mouth. The mouth is surrounded by a zone of large folds; more peripherally these

are abruptly replaced by much smaller papillae. At the ventral mid-point of the mouth, the snout is drawn out into a narrow fold ("pseudoproboscis") connecting to the right neck-lobe. On the ventral part of the neck, just behind the left part of the oral disc is a (sensory?) tubercle. Along the right side of the snout runs a low membrane, from the central side of the eye-lobe, to the right ventral corner of the oral disc. The gill was poorly preserved, but is long and bipectinate with osphradium on the ventral

face of the efferent membrane. There are no pallial margin tentacles or other appendages.

Operculum (Figure 16c). Brownish, multispiral, with central nucleus.

Radula (Figures 11a, b). n - 5 - 1 - 5 - n [n = 25–50, difficult to count], typical for the subfamily. The central and four inner lateral teeth are membranous, their apical half finely serrated. The outer lateral tooth, number 5, is more sturdily built and slightly smaller. The inner marginal tooth is sturdy and broad with about 10 small denticles along its apical third. The second marginal tooth is much more slender and slightly smaller; the third one and outward are simple and clawlike.

Jaw (Figure 14e). Rather thin and fragile, composed of numerous rodlets, dorsally and anteriorly deeply notched.

Remarks: Since no other species of *Falsimargarita* is known to be associated with hydrothermal vents or seeps, *F. nauduri* may be an occasional intruder. *Falsimargarita nauduri* resembles *F. georgiana* Dell, 1990 and *F. benthicola* Dell, 1990, but is proportionally taller and has a more circular cross section of the whorls.

Nothing is known about the biology of any species of *Falsimargarita*, and we were not able to find any stomach contents.

Fucaria Warén & Bouchet, 1993

Fucaria Warén & Bouchet, 1993:15.

Type species: *F. striata* Warén & Bouchet, 1993; by original designation; hydrothermal vents, JdF

Remarks: Warén & Bouchet (1993) classified *Fucaria* in the subfamily Halistylinae, but we now consider this uncertain.

The snout with its coat of sensory papillae may draw attention to the Solariellinae and Lirulariinae (cf. Hickman & McLean, 1990, fig. 79D, E), but in these groups the tentacles on the snout are much larger and true tentacles, with no apical tuft of sensory cilia. This is obvious in Hickman & McLean's (1990) fig. 79E, where the sensory papillae on the tentacles can be compared. We have not seen any comparably equipped snout among other "vetigastropods," and the character is a good apomorphy for *Fucaria*.

The new species below is quite similar to the type species and differs mainly in having a smooth shell. This is the third species of the genus, which now is known from the JdF, Florida Escarpment, and the south-western Pacific. (Inquiries about the whereabouts of the material from the Florida Escarpment have remained unanswered and the species therefore remains undescribed.)

Fucaria striata Warén & Bouchet, 1993

Fucaria striata Warén & Bouchet, 1993:16, figs. 9e–h, 12a–c, 13a–c, 38c.

New records: JdF, Middle Valley vent field: - ALVIN dive 3146, 10 spms (FMNH 280955).

Fucaria mystax Warén & Bouchet, sp. nov.

(Figures 8c, 11c, 12a–d, 16e)

Type material: Holotype and 2 paratypes in MNHN, 2 paratypes in V. Tunnicliffe reference collection.

Type locality: Off northeastern side of Papua New Guinea, 3 miles south of Lihir Island, Edison Seamount, 03°01.185'S, 152°03.492'E, 1483 m, 30-GTVA.

Material examined: Only known from the type material.

Distribution: Only known from the type locality.

Etymology: "Mystax," Greek, moustache, alluding to the coat of sensory papillae on the snout.

Description: *Shell* (Figure 8c). Rounded, skeneiform, sturdy, with thin, pale beige periostracum. The protoconch and apical whorls are lost by corrosion in all specimens. The teleoconch has more than 1.5 whorls, estimated to ca. 2.5 whorls. There is no sculpture, not even growth lines, except occasional scars from earlier damage to the outer lip. The periostracum is smooth and very thin. The peristome is not thickened in any specimen, almost round, not indented by the preceding whorl, more tangential than radial and prosocline. The umbilicus is deep and narrow, barely visible in a basal view.

Dimensions. Maximum diameter 5.8 mm.

Soft parts (Figures 12a–d). The foot is large and flat with well demarcated propodium, truncate anteriorly with the corners drawn out to small tentacles and paralleled by the propodium. Each side of the foot has more than three epipodial tentacles. The head is quite large, the snout cylindrical with the apical part demarcated by a rounded swelling. The mouth is centrally situated in the flat extremity of the snout. The cephalic tentacles are rather short, of similar length as the snout, and encircled, except antero-ventrally, by a ridge, perhaps a modified combination of cephalic lappet and eye-lobe. Eyes not seen. The right neck-lobe consists of two flat tentacles, the left one probably a single large one which apically is split in two or three parts. The cephalic tentacles are anteriorly (Figure 12d) and posteriorly covered by a dense coat of sensory papillae, up to 100 µm long, as is the apical part of the snout. The gill is monopectinate, attached in its whole length, and has sensory bursicles.

Operculum (Figure 16e). It is yellowish, rather stiff, multispiral with about 10 whorls, it has a central nucleus, short growth zone, and indistinct sculpture of growth lines. There is a slight overlap of the edge of the preceding whorl.

Radula (Figure 11c). n - 11 - 1 - 11 - n. The central tooth is short with a drawn out, narrow anterior support,

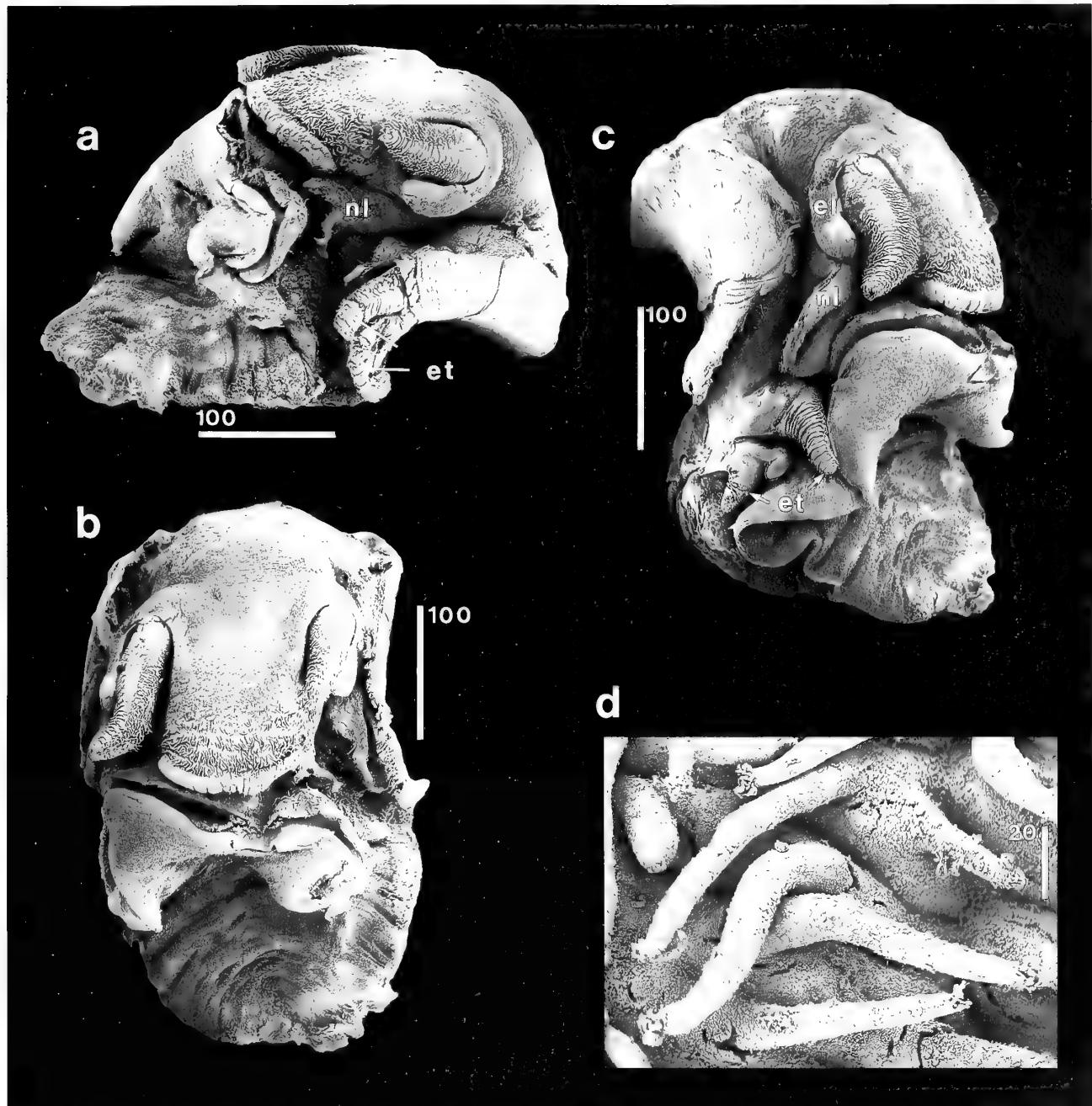


Figure 12. *Fucaria mystax* Warén & Bouchet, sp. nov., holotype, critical-point dried. *a*. Head-foot, left side. *b*. Head-foot, front view. *c*. Head-foot, right side. *d*. Sensory papillae from snout. el - eye-lobe; et - epipodial tentacle; nl - neck-lobe. Scale bars in μm .

sturdy shaft, and smooth edge of the apical plate. The lateral teeth are tightly packed, interlocking along most of their length, and only the outermost two teeth have a denticulate apical plate. The marginals form an almost unbroken continuation of the laterals but differ in having a strong tubercle below the denticulate apical plate.

Remarks: The few specimens had been preserved in a mixture of methanol and vodka (Tunnicliffe, 1994), but some detail can be seen from the critical-point dried body. The neck-lobes may be broken or deeply split, this could not be decided because their epithelium was peeling badly.

Family SKENEIDAE Clark, 1851

Protolira Warén & Bouchet, 1993*Protolira* Warén & Bouchet, 1993: 22.

Type species: *P. valvatooides* Warén & Bouchet, 1993; by original designation; hydrothermal vents, MAR, Snake Pit.

Remarks: A second species, *P. thorvaldssoni* Warén, 1996, was recently described from decaying whale bone off south-western Iceland, and turned out to be very common at Lucky Strike. The two species are quite similar, and the poor condition of most adult specimens makes it more difficult to separate them. *Protolira valvatooides* does, however, have a thick, tough, shiny, and dark olive green periostracum, the shell has a slightly more depressed shape, and a narrow, brown line parallels the pallial margin, about 0.1 mm behind it. This line is missing in *P. thorvaldssoni*.

Warén & Bouchet (1993: fig. 18D) figured what they assumed to be the protoconch of *Protolira valvatooides*, but that was a very young specimen of what we here describe as *Lirapex costellata* (not known then), a mistake we realized only after finishing this manuscript, when some very young specimens became available from particle traps. The protoconch of *Protolira* actually is similar to that of *Bruciella* (Figure 15E), with the same kind of spiral sculpture and sharp incremental line after 1/20 of a teleoconch whorl.

Protolira valvatooides Warén & Bouchet, 1993*Protolira valvatooides* Warén & Bouchet, 1993: 20, figs. 17A–B, 18D, G, 19A–C, 20A–F

New records: MAR, Menez Gwen: DIVA, 1.13 on an active chimney, 19 spms; - DIVA 1 PL 14, on sulfide rock with Hydrozoa, 36 spms; - DIVA 1 PL 16, on base of a black smoker, 1 young; - DIVA 2 PL 11, 12 spms; on mussels, 11 spms; on rocks, 131 spms; suction sample among mussels, 3 spms; - DIVA 2 PL 12, 524 spms; suction sample among mussels, 8 spms; - DIVA 2 PL 13, 2 suction samples among mussels, 5 and 7 spms; - DIVA 2 PL 14, 6 spms; - DIVA 2 PL 16, 77 spms; - MARVEL PL1201, 850 m, 3700 spms; - MARVEL PL1202, 850 m, suction sample, 50 spms; among mussels, 1637 spms; retrieval box, 1130 spms; - MARVEL PL1203, 850 m, retrieval box, 895 spms; - MARVEL PL1208, 850 m, retrieval box, 17 spms; - MARVEL PP10, particle trap, 15 spms, 3 protoconchs; - MARVEL PP49, particle trap, 4 spms; - MARVEL PP50, particle trap, 6 spms, 3 protoconchs; - MARVEL PPS 20, particle trap, 13 spms, 3 protoconchs. *Lucky Strike:* DIVA 1 PL 18, among mussels, 1 spm; - DIVA 2 PL 02, 3 spms; - DIVA 2 PL 03, 1 spm; DIVA 2 PL 07, 3 spms; - DIVA 2 PL 19, 7 spms; - DIVA 2 PL 20, 4 spms; - ALVIN dive 2606, 5 spms; - LUSTRE Exp., Tour Eiffel, on mussels, 2 spms; - MAR-

VEL PL1191, Bairro Alto, retrieval box, 1 spm; 2 suction samples, 1 spm each; - MARVEL PL1193, Bairro Alto, 1585 m, retrieval box, 8 spms; - MARVEL PL1194, Tour Eiffel, retrieval box, 4 spms; - MARVEL PL1195, Tour Eiffel, 1685 m, retrieval box, 3 spms; - MARVEL PL1200, Bairro Alto, 0.25 m² rock surface close to edifice, 4 spms; - MARVEL PL1205, Bairro Alto + Tour Eiffel (mixed), 1700 m, 5 spms.

Distribution: MAR from Menez Gwen to Lucky Strike, in ca. 850–1800 m depth, living among mussels, in sediment and on rocks.

Remarks: *Protolira valvatooides* is one of the most common gastropods at Menez Gwen. It reaches a maximum size of 3.5 mm. Most of the spire is usually corroded away, and in extreme cases the body may consist of half a whorl with the digestive gland and gonad remaining as a very short $\frac{1}{10}$ of a whorl. The gut contains mixed sediment.

When we originally described *P. valvatooides*, we had two complete and several decalcified specimens. We are therefore not certain that the original illustrations of the radula and soft parts are based on *P. valvatooides*. We have now examined radulae and critical point dried specimens of both *valvatooides* and *thorvaldssoni* and have found no differences in the external morphology of the soft parts, except that *P. valvatooides* has a sharp reddish brown line paralleling the pallial margin. There is a tendency that *P. thorvaldssoni* has a more well demarcated unpaired cusp on the central radular tooth, but this was not always the case when we examined 15 radulae of each species. Some specimens of *thorvaldssoni* had a poorly defined cusp, while no specimen of *valvatooides* had a well defined one. Our (1993: fig. 19A–B) therefore is probably based on *P. thorvaldssoni*.

Protolira thorvaldssoni Warén, 1996*Protolira thorvaldsoni* Warén, 1996: 201, figs. 3E–F, 4A–D (incorrect original spelling).

New records: Menez Gwen: DIVA 1 PL 13 on an active chimney, 2 spms; - DIVA 1 PL 14, on sulfide rock with Hydrozoa, 6 spms; - MARVEL PL1201, 850 m, 3 spms; - MARVEL PL1203, 850 m, retrieval box, 9 spms. *Lucky Strike:* DIVA 1 PL 01, among mussels, 1 spm; - DIVA 1 PL03(1), 7 spms; - DIVA 1 PL 04, in baited trap, 4 spms; on inactive chimney among Hydrozoa and sponge *Cladorhiza*, 39 spms; - DIVA 1 PL 17, among mussels, 6 spms; - DIVA 1 PL 19, among mussels, 6 spms; DIVA 2 PL 02, 34 spms; on chimney, 3 spms; - DIVA 2 PL 03, 52 spms; - DIVA 2 PL 04, 58 spms; 2 suction samples among mussels in shimmering water, 12 and 39 spms; - DIVA 2 PL 05, 9 spms; - DIVA 2 PL 06, 2 spms; - DIVA 2 PL 07, 84 spms; 3 suction samples among mussels and hydrothermal sediments, 9, 3, and 12 spms; - DIVA 2 PL 08, in retrieval box, 16 spms; 2 suction samples among

mussels and hydrothermal sediments, 2 and 7 spms; - DIVA 2 PL 09, 8 spms; suction sample among mussels and hydrothermal sediments, 1 spm; - DIVA 2 PL 10, 104 spms; on rocks, 5 spms; 2 suction sample among mussels and hydrothermal sediments, 5 and 14 spms; in retrieval box, 1750 spms; - DIVA 2 PL 17, 6 spms; - DIVA 2 PL 19, 17 spms; - DIVA 2 PL 20, 562 spms; - DIVA 2 PL 21, 30 spms; - DIVA 2 PL 25, 66 spms; - DIVA 2 PL 26, 72 spms; Sintra site, 1 spm; - DIVA 2, in particle trap, 1 spm; - ALVIN dive 2606, 20 spms; - ALVIN dive 2607, 187 spms; - LUSTRE Exp., Sintra site, on mussels, 51 spms; - MARVEL PL1191, Bairro Alto, retrieval box, 28 spms; 1 suction sample, 1 spm; - MARVEL PL1192, Bairro Alto, retrieval box, 1630 m, 5 spms; - MARVEL PL1193, Bairro Alto, 1585 m, retrieval box, 44 spms; - MARVEL PL1194, Tour Eiffel, retrieval box, 98 spms; - MARVEL PL1195, Tour Eiffel, 1685 m, retrieval box, 141 spms; - MARVEL PL1200, Bairro Alto, 0.25 m² rock surface close to edifice, 90 spms; - MARVEL PL1205, Bairro Alto, retrieval box, 23 spms; Bairro Alto + Tour Eiffel (mixed), 1700 m, 59 spms; - MARVEL PP49, particle trap, 2 spms. *Rainbow*: MARVEL PL1196, among mussels, 2300 m, 13 spms. *Snake Pit*: ALVIN dive 2615, 6 spms; - ALVIN dive 2617, 5 spms; - ALVIN dive 2619, 15 spms; - ALVIN dive 2622, 1 spm.

Distribution: MAR from Menez Gwen to Snake Pit, in ca. 850–3700 m depth, living among mussels, in sediment and on rocks; also off south-western Iceland, ca. 63°N, in a few hundred meters depth, on whale bone.

Remarks: *Protolira thorvaldssoni* is very common at Lucky Strike, much more so than *P. valvatoides*. It attains a maximum shell diameter of 4.2 mm. Some specimens from Lucky Strike had a small syllid polychaete in the umbilicus. The gut contains mixed sediment.

The spire is usually partly corroded away, but less so than in *P. valvatoides*. This may be the result of a slight difference in preferred micro habitat, since *P. valvatoides* has a thicker and presumably more protective periostracum.

Protolira thorvaldssoni is one of the few species known both in hydrothermal vents and outside them, and it is significant that it was described from a biogenic substrate. The two specimens that formed the base for the original description were not very well preserved, and the identification may be questioned, but they are more similar to each other than to two more species of the same group (undescribed) from off western Europe, with a radula with a more normal skeneid type central field.

In the original description, the specific epithet was spelled *thorvaldsoni* but the species was said to be named after Mr Jón Thorvaldsson. This is an incorrect original spelling in the sense of Art. 32.5 of the Code, and the spelling *thorvaldssoni* is a justified emendation.

Bruceiella Warén & Bouchet, 1993

Bruceiella Warén & Bouchet, 1993:26.

Type species: *B. globulus* Warén & Bouchet, 1993; by original designation; vents in the North Fiji Basin.

Bruceiella athlia Warén & Bouchet, sp. nov.

(Figures 8d, 11d–f, 13a–d, 15e, 16j)

Type material: Holotype SMF 311982 and 50+ paratypes SMF311983; 50+ paratypes in MNHN.

Type locality: Aleutian Trench, Shumagin site, 54°18'N, 157°12'W, 4808 m (TVGKG 40), 180 spms and shs.

Material examined: The types and: *Aleutian Trench*: - TVGKG 49, 16 shs and spms.

Distribution: Only known from the Aleutian seeps, Shumagin site, at about 4800 m.

Etymology: “*athlios, -a*,” Greek, miserable, referring to the sad condition of all adult specimens.

Description: *Shell* (Figure 8d). Fairly sturdy, opaque greyish, tall skeneiform, always badly corroded and only in juvenile specimens, more than half an intact whorl. The protoconch (Figure 15e) has about ⅓ of a whorl, a diameter of 450 µm, and its initial part is sculptured by a system of low, raised ridges forming an irregular net. More distally these ridges get a mainly spiral orientation and finally they fade out, well before the end of the protoconch. The transition to the protoconch is marked by a sharp and narrow furrow, followed by a short, smooth area and a varix. The teleoconch is almost smooth, except irregular and indistinct incremental lines. The shape of the shell is difficult to reconstruct, but without interference of corrosion it may have been more tall spired than the type species. The peristome is prosocline, more tangential than radial, round, and not indented by the preceding whorl. An umbilicus is probably present in undamaged specimens but it is probably narrow.

Dimensions. Maximum diameter 2.3 mm.

Soft parts (Figures 13a–d). The pallial cavity comprises almost half a whorl, and its margin is smooth. The single gill is monopectinate, has ca. 20–25 leaflets and is situated in the left half. The presence of sensory bursicles could not be verified, because of problems with mucus. The head-foot is well developed, with a slightly tapering snout and a mainly ventrally situated mouth. The cephalic tentacles are distinctly shorter than the snout when contracted, laterally richly beset with sensory papillae (Figure 13c), have an indistinct basal ventral sheath, and lack eyes. Behind the right cephalic tentacle follows a smooth, claviform and a larger, irregularly shaped, laterally ciliated, fingerlike appendage (“neck tentacles”). Ventrally to the left cephalic tentacle is a large, partly ciliated appendage. The foot is large and flat, posteriorly rounded,

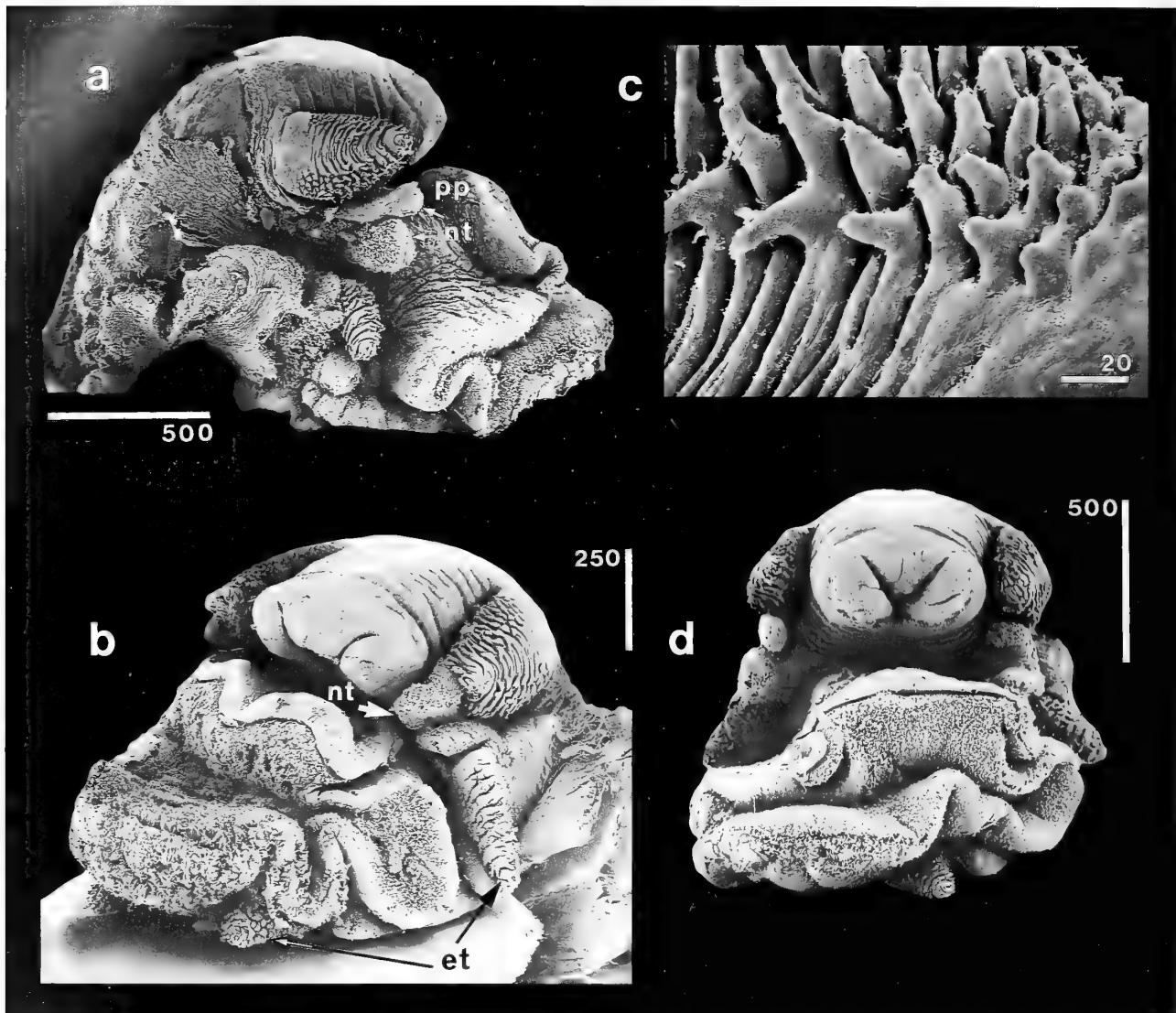


Figure 13. *Bruceiella athlia* Warén & Bouchet, sp. nov., critical-point dried, Aleutian Seeps, Shumagin site. a. right side of head-foot. b. Anterolateral view, left side, of head-foot. c. Detail of cephalic tentacle. d. Head-foot, front view. et - epipodial tentacle; nt - neck tentacle; pp - propodium. Scale bars in μm .

anteriorly truncate, and its corners are drawn out to short tentacles, paralleled by the propodium. The right epipodial arrangement consists of at least four tentacles; the left one seems to have one tentacle less.

Operculum (Figure 16j). Highly multispiral, dull, and opaque with central nucleus.

Radula (Figures 11e, f). n - 4 - 1 - 4 - n, long and slender; sac with bilobed end. The central tooth has a smooth, triangular apical plate; broad, winglike laterobasal processes; and a central projecting ridge. The four laterals are uniformly shaped, with a distinct, basal "elbow" and a weakly serrate, apical triangular plate. The innermost marginal has a lateromarginal plate demarcating its field; the tooth is slender, has a laterally flattened

shaft and a notch below the hand-shaped, "7-fingered" apical plate. The second to eighth marginals (Figure 11f, number 6) resemble the first; farther laterally the marginals become more slender with finer and more numerous denticles, a less defined apical plate, and end up as simple membranous "ribbons."

Remarks: *Bruceiella athlia* closely resembles *B. globulus*, but is larger and has a much broader central tooth in the radula. The central tooth of *B. globulus* also lacks the transverse basal ridge. The outermost whorl of the operculum corresponds to 6% of the diameter in *B. athlia*, 10% in *B. globulus*, which means that it is almost twice as tightly coiled.

Entoprocts are often attached along the edge of operculum. The gut was filled by detritus.

Superfamily LEPETODRILOIDEA McLean, 1988

Remarks: The systematic position of the lepetodriloids has varied in the literature (McLean, 1988; Haszprunar, 1988; Ponder & Lindberg, 1997; Warén, in press). We follow the classification proposed by Warén (in press), to which we refer for more detailed information.

Family SUTILIZONIDAE McLean, 1989

Remarks: Warén (in press) raised Sutilizoninae to family level to make it equivalent with its assumed sister taxon Lepetodrilidae. At the same time *Temnocinclus* and *Temnozaga* were placed in Sutilizonidae, without any subfamily grouping because of lack of information on some characters.

Sutilizona McLean, 1990

Sutilizona McLean, 1989a:14.

Type species: *S. theca* McLean, 1989; by original designation; EPR, on sulfide mounds near 12°N.

Remarks: *Sutilizona* is now known from the three species below, from the EPR, the JdF, and the MAR. They all share the same shell shape, radular morphology, and protoconch.

Sutilizona theca McLean, 1989

(Figures 17f, i)

Sutilizona theca McLean, 1989a: 15, figs. 3A–C, 4D–F, 5E–F

New records: EPR at 13°N: - HERO 92 dive 2522, 5 spms.

Distribution: EPR, 12–13°N, 2500–2700 m.

Remarks: The largest of the new specimens has a maximum diameter of 2.4 mm; previously recorded maximum size was 1.3 mm. The sculpture varies considerably (Figures 17f, i); some have a much finer sculpture, but the largest specimen, which regrettably was broken, starts out with a coarse sculpture and changes to much finer. *Sutilizona tunnicliffae* differs from *S. theca* in having weaker axial sculpture and distinct spiral sculpture.

Sutilizona pterodon Warén & Bouchet, sp. nov.

(Figures 15g; 17c, e, g, h; 18a, f)

Type material: Holotype and 5 paratypes in MNHN.

Type locality: MAR, Snake Pit, Ruches or Elan, ALVIN dive 2619, 23°22.13'N, 44°57.13'W, 3490–3520 m.

Material examined: The types and: MAR at Snake Pit: - ALVIN dive 2613, 2 spms; - ALVIN dive 2617, 4 spms; HYDROSNAKE PL 10, retrieval box, 6 spms (shells dissolved).

Distribution: Only known from the MAR, Snake Pit, depth 3470–3520 m.

Etymology: From Greek “pteros” wing and “odus” teeth, referring to the winglike outer marginal teeth.

Description: *Shell* (Figures 17c, e, g, h). Fragile, white with a thin periostracum and covered by thick deposits of bacterially precipitated iron and manganese oxides. The protoconch (Figure 15g) consists of about half a whorl with poorly defined coiling sculptured with strong pits of a diameter of 1–4 µm and to some extent arranged to form a spiral pattern. The diameter is 200 µm, and the protoconch is conspicuously protruding in an apertural view (Figure 15g), although it usually is completely concealed by the deposits. The teleoconch consists of up to 1.2 whorls of rapidly increasing diameter. Initially it is sculptured only by coarse and irregular growth lines; at the beginning of the slit, after ca. ½ a whorl; also some spiral ribs of varying size develop and form an indistinct and irregular network on the last half whorl. Frequently the intersections of the spiral and axial sculpture form small, almost spinelike tubercles. The basal surface of the shell is demarcated by an indistinct keel. The slit is open for a length of about ⅓ of the shell, its earlier part is filled by small scalelike incremental lamellae. The umbilicus is deep and widely open.

Dimensions. Maximum diameter of shell 2.0 mm (holotype).

Operculum extremely thin, membranous, transparent, multispiral with central nucleus and kept folded double in crawling position.

Radula (Figures 18a, f). Similar to *S. theca*, but the central tooth is more narrow. The lateral and marginal fields can hardly be distinguished, but the two fields form a continuous series of laterally more slender and simplified teeth. The outermost marginal tooth is conspicuous in successful preparations, broadly fan-shaped, and with an inner fused tooth looking like a shepherd's crook.

Soft parts. The foot is thick and muscular, simple, anteriorly bluntly rounded, posteriorly more pointed; propodium not visibly set off. The foot has one pair of epipodial tentacles, placed just behind the anterior margin of the operculum. The head is large, with a pair of slender, tapering cephalic tentacles, posteriorly directly followed by an inconspicuous eye-lobe (without eye); no other appendages. The snout is short, slightly tapering, with ventral mouth. The left gill is small, monopectinate with seven leaflets; the right gill is reduced to a group of five small appendages at the extreme part of the corner formed between the slit and the adjoining pallial margin. The length of the gill slit corresponds to ⅓ of the depth

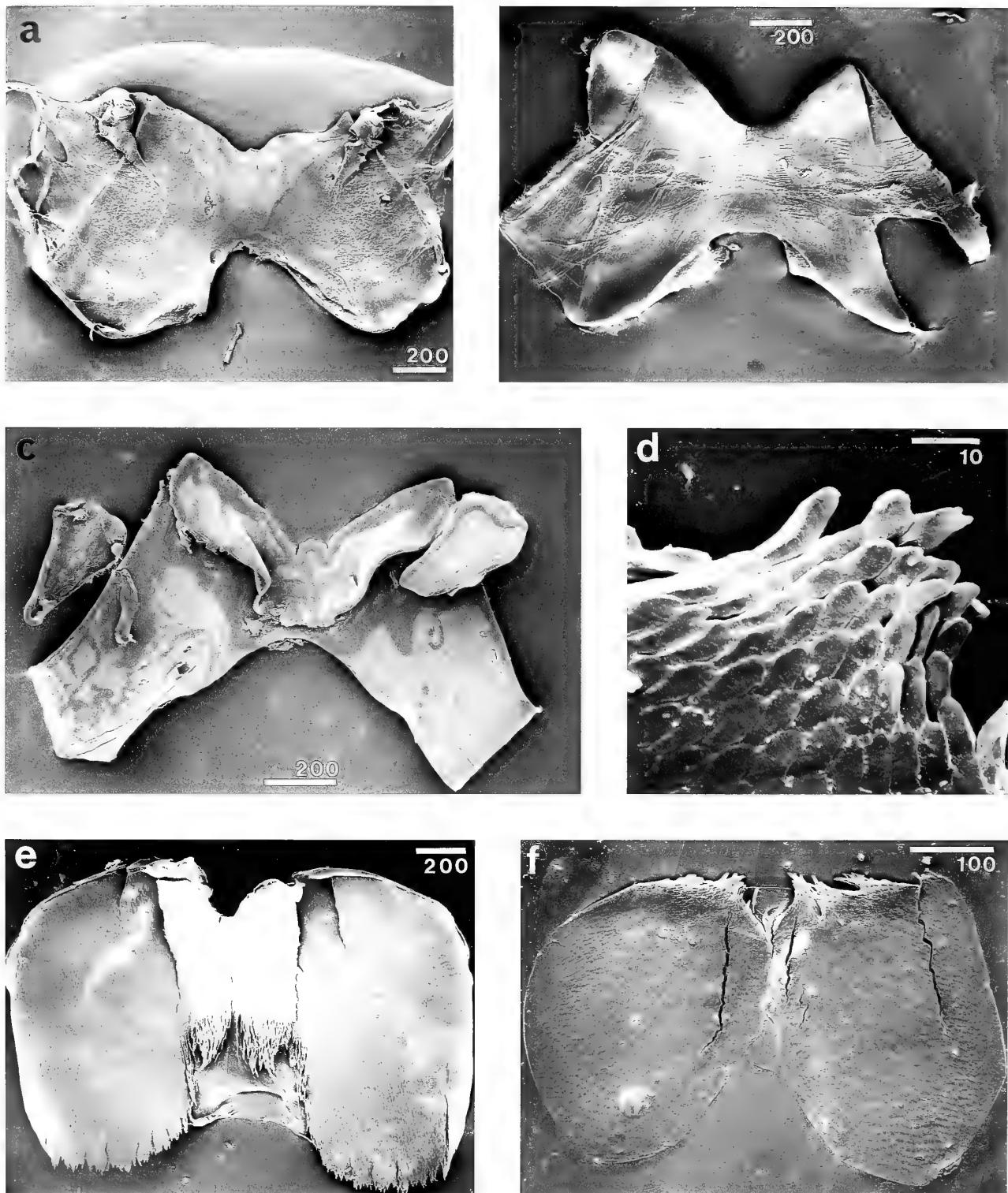


Figure 14. Jaws. a, b. *Neolepetopsis ferrugivora* Warén & Bouchet, sp. nov., MAR, Lucky Strike. a. Inside. b. Outside. c. *Eulepetopsis vitrea*, EPR, 13°N, inside. d, f. *Lepetodrilus atlanticus* Warén & Bouchet, sp. nov., MAR, Lucky Strike. e. *Falsimargarita nauduri* Warén & Bouchet, sp. nov., holotype. Scale bars in μm .

of the pallial cavity; its sides are furnished with two or three broad and low papillae, basally in the slit is a longer, cylindrical tentacle. There are no sensory papillae anywhere on the body, and the presence of ctenidial bursicles could not be verified.

Remarks: *Sutilizona pterodon* differs from *S. theca* and *S. tunnicliffae* in never closing the slit (if our specimens are adult), in having weaker sculpture and in not developing the distinct corner of the teleoconch at the slit. It differs also in its peculiar outer marginal radular teeth. *Sutilizona tunnicliffae* instead has its outermost four to five marginals much broader and simpler than usual (Figure 18g). The fan-shaped outer marginal can therefore hardly be considered more than a specific apomorphy.

Sutilizona tunnicliffae Warén & Bouchet, sp. nov.

(Figures 15f; 17d; 18b, d, g)

Type material: Holotype destroyed during examination.

Type locality: JdF, Endeavour Segment: - ROPOS #278, fissure at Main Field, 47°56.9'N, 129°06.9'W, 2202 m.

Material examined: Only known from the type locality.

Distribution: Only known from the type locality.

Etymology: Named after Verena Tunnicliffe.

Description: Shell (Figure 17d). Fragile, white with a thin periostracum and covered by thin deposits of iron oxides. The protoconch (Figure 15f) consists of about half a whorl with poorly defined coiling sculptured with strong pits of a diameter of 1–4 µm and to some extent arranged to form a spiral pattern. The diameter is uncertain because of corrosion but has been within the range 165–220 µm. The protoconch is conspicuously protruding in an apertural view. The teleoconch consists of up to 1.1–1.3 whorls of rapidly increasing diameter. Initially it is sculptured only by coarse and irregular growth lines; at the beginning of the slit, after ca. ¼ of a whorl, also some spiral ribs of varying size develop and form an indistinct and irregular network on the last half whorl. The slit is open for a length of about ⅓ of the shell, its earlier part is filled by small scalelike incremental lamellae. The umbilicus is deep and widely open.

Dimensions. Maximum diameter of shell 2.2 mm (holotype).

Oberculum extremely thin, membranous, transparent, with central nucleus.

Radula (Figures 18b, d, g). Similar to *S. theca*, but the lateral field is more demarcated. The outermost marginals (Figure 18g) consist of a series of simple and flat teeth with a weak apical crenulation and small basal angle. The demarcation between the lateral and marginal field is unclear, but there are at least two unquestionable lateral teeth. The central tooth is low and broad with three denticles at each side of the main cusp.

Remarks: We have only seen a single, slightly damaged specimen of this species and would probably not have described it, if it did not so nicely show the scissurellid affinities in radular characters. Regrettably the specimen was badly broken when dismounted from the stub.

Temnocinclus McLean, 1989

Temnocinclus McLean, 1989:5.

Type species: *T. euripes* McLean, 1989; by original designation; hydrothermal vents at JdF.

Temnocinclus euripes McLean, 1989

Temnocinclus euripes McLean, 1989a: 7, figs. 1A–H, 4A, 5A–B.

Temnocinclus euripes: Haszprunar, 1989b: 3, fig. 1; Warén, in press.

New records: JdF, Explorer Ridge: - ROPOS 284, on a chimney top, 5 spms (Tunnicliffe ref. coll., 1 in MNHN). Megaplume South: - ALVIN dive 2078, 6 spms (Tunnicliffe ref. coll., 3 in MNHN).

Distribution: JdF, at ca. 44–50°N, in ca. 1500–2300 m.

Remarks: There are still some problems with the systematic position of this species (Warén in press), due to lack of well fixed specimens.

Family LEPETODRILIDAE McLean, 1988

Lepetodrilus McLean, 1988

Lepetodrilus McLean, 1988:6.

Type species: *L. pustulosus* McLean, 1988; by original designation; vents at the EPR.

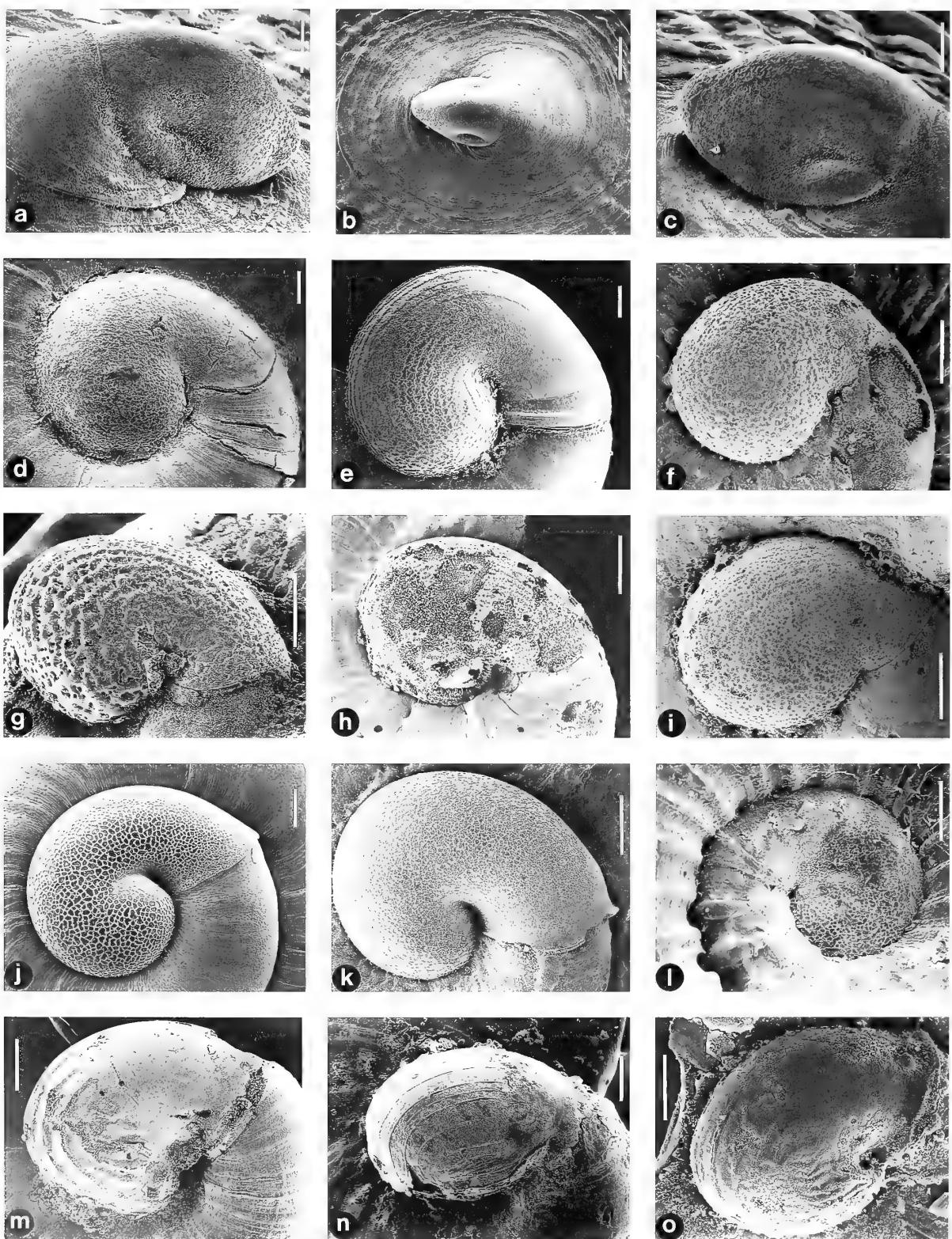
Remarks: The species of *Lepetodrilus* form a morphologically uniform group with only slight variation in shell and gill morphology. Some are difficult to identify as young at the EPR where there may be up to four sympatric species, and we figure a set of young specimens (Figures 22a–e) of the size when they give rise to problems. The species of *Lepetodrilus* often totally dominate the gastropod fauna of the vents at the EPR and MAR. A large sampling at 13°N contained the four species, of which *L. elevatus* formed 91% and the four together 93% of 176.000 specimens.

Lepetodrilus atlanticus Warén & Bouchet, sp. nov.

(Figures 14d, f, 15i, 19a–f, 20a–d, 21a, b)

Type material: Holotype and ca. 9500 paratypes in MNHN.

Type locality: MAR, Menez Gwen, DIVA 2 PL 16, 37°50.54'N, 31°31.30'W, 860–870 m.



Material examined: The type material and: MAR, Menez Gwen: - DIVA 1 PL 13, 1 spm; on active chimney, 38 spms; - DIVA 1 PL 14, on sulfide rock with Hydrozoa, 14 spms; - DIVA 1 PL 16, on base of a black smoker, 19 young; - DIVA 2 PL 11, on mussels, 606 spms; on blocks, 349 spms; suction sample among mussels, 10 spms; - DIVA 2 PL 12, 312 spms; 3 suction samples among mussels, 114, 127, and 149 spms; - DIVA 2 PL 14, 22 spms; suction sample among mussels, 43 spms; on mussels, 78 spms; - MARVEL PL1201, 850 m, 23,950 spms; - MARVEL PL1202, 850 m, suction sample, 722 spms; among mussels, 1700 spms; retrieval box, 1374 spms; - MARVEL PL1203, 850 m, retrieval box, 1804 spms; - MARVEL PL1208, 850 m, retrieval box, 33 spms; - MARVEL PP49, particle trap, 4 spms. Lucky Strike: - DIVA 1 PL 01 among mussels, 6 spms; - DIVA 1 PL 03, 8 spms; - DIVA 1 PL 04, on inactive chimney among Hydrozoa and the sponge *Cladorhiza*, 11 spms; - DIVA 1 PL 09, 21 spms; - DIVA 1 PL 17, among mussels, 90 spms; - DIVA 1 PL 18, among mussels, 1 spm; - DIVA 1 PL 19, among mussels, 10 spms; - DIVA 2 PL 01, 3 spms; - DIVA 2 PL 03, 7 spms; - DIVA 2 PL 04, 13 spms; suction sample among mussels in shimmering water, 5 spms; - DIVA 2 PL 05, 2 young; - DIVA 2 PL 06, 3 spms; - DIVA 2 PL 07, 3 young; 2 suction samples among mussels and hydrothermal sediment, 4 and 2 spms; on mussels, 2 spms; - DIVA 2 PL 08, 11 spms; 2 suction samples among mussels and hydrothermal sediments, 1 spm and 1 young; - DIVA 2 PL 09, 2 spms; suction sample among mussels and hydrothermal sediments, 3 spms; - DIVA 2 PL 10, 10 spms; on a rock, 21 spms; 2 suction samples among mussels and hydrothermal sediments, 1 and 10 spms; in retrieval box, 286 spms; - DIVA 2 PL 17, 33 spms; - DIVA 2 PL 19, 5 spms; - DIVA 2 PL 20, 78 spms; - DIVA 2 PL 21, 8 spms; - DIVA 2 PL 25, 8 spms; - DIVA 2 PL 26, 272 spms; - ALVIN dive 2605, 8 spms; - ALVIN dive 2606, 7 spms; - LUSTRE Exp., Tour Eiffel, on mussels, 10 spms; Sintra site, on mussels, 24 spms; - MARVEL PL1191, Bairro Alto, retrieval box, 3 spms; - MARVEL PL1192, Bairro Alto, retrieval box, 1630 m, 4 spms; - MARVEL PL1193, Tour Eiffel, retrieval box, 19 spms; - MARVEL PL1194, Tour Eiffel, retrieval box, 14 shs; - MARVEL PL1195, Tour Eiffel, retrieval box, 29 spms; - MARVEL PL1200, Bairro Alto, 0.25 m² rock surface close to edifice, 14

spms; - MARVEL PL1205, Bairro Alto, retrieval box, 10 spms; - MARVEL PL1206, retrieval box, 1700 m, 1 spm. Snake Pit: - ALVIN dive 2615, 15 spms.

Distribution: MAR, between 38°N and 23°N, in 850–3500 m depth. Mainly found on mussels and rocks in the vicinity of vents, usually in large quantities.

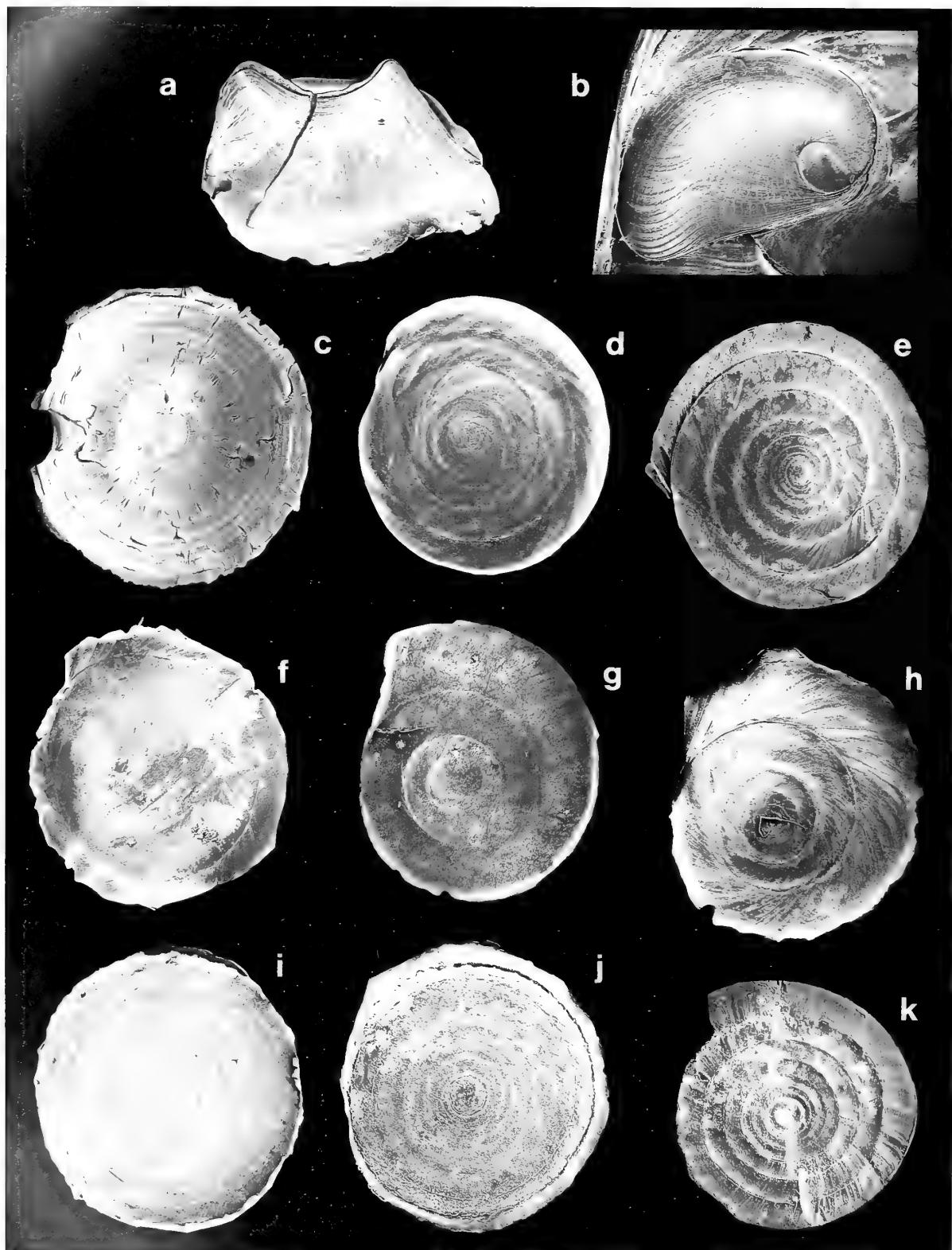
Etymology: “*atlanticus*” alluding to it being the first species of its genus known from the Atlantic.

Description: *Shell* (Figures 19a–f). Small for the genus, brownish-greenish, rather fragile, ovate and elevated limpet-shaped with overhanging initial part. Protoconch (Figure 15i) irregularly shaped, spirally coiled, but without defined suture. The sculpture consists of irregular, spirally arranged ridges and pits, diameter about 1–4 µm. The maximum diameter of the protoconch is 200 µm. The teleoconch consists of about 1.25 whorls of rapidly increasing diameter, tightly joined to earlier ones, and forming a columellar shelf. The whole shell is covered by a tough, greenish-brownish periostracum, which extends about $\frac{1}{12}$ the width of the aperture across the calcareous peristome. The muscle scars are well demarcated in adult specimens, equally developed on both sides, reach the anterior $\frac{1}{4}$ of the shell and cross the columellar shelf as a narrow line.

Dimensions. Maximum shell length 7.2 mm.

Soft parts (Figures 20a–d). The foot is rounded, anteriorly somewhat truncated and with a distinctly set-off propodium. It is surrounded by an epipodial membrane with one pair of triangular processes on each side at the posterior $\frac{1}{3}$ and a single such process below the anterior part of the shell muscle. The membrane continues anteriorly as a ridge, turns across the shell muscle, and ends in the pallial cavity, when reaching the lateroventral part of the neck. The pallial margin is bilobed, with an inner crenulated lobe, demarcated by a deep fissure where the periostracum is produced. The head is large, with a slightly tapering snout, apical demarcating ridge, and apical-ventral mouth. The cephalic tentacles are conical, slightly longer than the snout in preserved specimens; their base is encircled, ventrally and laterally by a skin flap (tentacle collar). Both males and females have a simple appendage, latero-ventrally at the right base of the snout. The size is variable, from a small plough-shaped skin fold in fe-

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Figure 15. Protoconchs. a–c. *Neolepetopsis densata*, EPR, 13°N. d. *Sahlingia xandaros* Warén & Bouchet, gen. & sp. nov., Aleutian Seeps, Shumagin site. e. *Bruceiella athlia* Warén & Bouchet, sp. nov., Aleutian Seeps, Shumagin site. f. *Sutilizona tunnicliffae* Warén & Bouchet, sp. nov., holotype. g. *S. pterodon* Warén & Bouchet, sp. nov., MAR, Menez Gwen. h. *Pseudorimula midatlantica*, MAR, Lucky Strike. i. *Lepetodrilus atlanticus* Warén & Bouchet, sp. nov., MAR, Menez Gwen. j. *Retiskenea diploura* Warén & Bouchet, gen. & sp. nov., Aleutian Seeps, Shumagin site. k. *Melanodrymia galeronae* Warén & Bouchet, sp. nov., holotype. m. *Lirapex costellata* Warén & Bouchet, sp. nov., paratype. n. *Adeuomphalus trochanter* Warén & Bouchet, sp. nov., holotype. o. *Depressigyrta globulus*, JdF, Fairy Castle Vent site. Scale bars 50 µm, except Figure b, which is 100 µm.



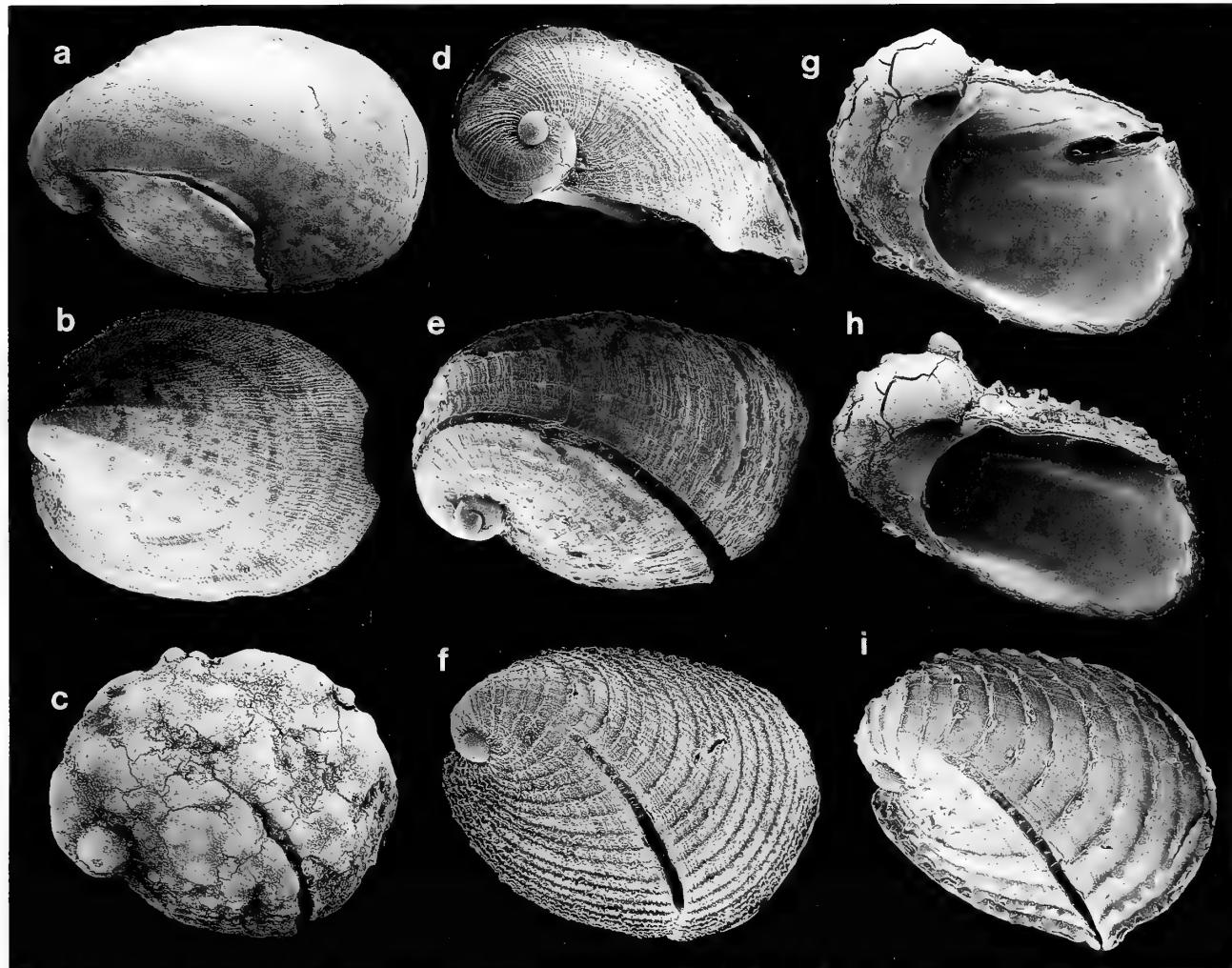


Figure 17. *Gorgolepis* and *Sutilizona*, shells. a. *G. spiralis*, EPR, 13°N, diameter 3.5 mm. b. *G. emarginatus*, EPR, 13°N, diameter 5.4 mm. c. *S. pterodon* Warén & Bouchet, sp. nov., MAR, Lucky Strike, shell not cleaned, diameter 2.2 mm. d. *S. tunnicliffae* Warén & Bouchet, sp. nov., holotype, diameter 2.2 mm. e. *S. pterodon* Warén & Bouchet, sp. nov., MAR, Lucky Strike, diameter 2.2 mm. f. *S. theca*, EPR, 13°N, diameter 1.8 mm. g, h. *S. pterodon* Warén & Bouchet, sp. nov., MAR, Lucky Strike, diameter 1.7 mm. i. *S. theca*, EPR, 13°N, diameter 1.5 mm.

males, to comparable to that of the snout in males. A ciliated tract starts from an area one tentacle length posterior to this process, extends forward, covering much of the dorsal side of the organ, and ends between the ap-

pendix and the tentacle collar. In males the appendage has a dorsal groove, which continues across the right side of the neck backward to the male pore. At the left ventral side of the neck is a small short tentacle or papilla, as-

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Figure 16. Opercula. a, b. *Shinkailipas briandi* Warén & Bouchet, sp. nov., MAR, Lucky Strike, maximum diameter 3.8 mm b. Detail showing the operculum of the settling veliger, diameter 0.55 mm c. *Falsimargarita nauduri* Warén & Bouchet, sp. nov., holotype, diameter 4.9 mm. d. *Adeuomphalus trochanter* Warén & Bouchet, sp. nov., holotype, diameter 1.05 mm. e. *Fucaria mystax* Warén & Bouchet, sp. nov., holotype, diameter 3.3 mm. f. *Melanodrymia galeronae* Warén & Bouchet, sp. nov., paratype, diameter 1.07 mm. g. *Retiskenea diploura* Warén & Bouchet, gen. & sp. nov., holotype, diameter 0.76 mm. h. *Sahlingia xandaros* Warén & Bouchet, gen. & sp. nov., Aleutian Seeps, Edge site, diameter 3.5 mm. i. *Lirapex costellata* Warén & Bouchet, sp. nov., MAR, Lucky Strike, diameter 2.0 mm. j. *Bruceiella athlia* Warén & Bouchet, sp. nov., Aleutian Seeps, Shumagin site, diameter 1.5 mm. k. *Peltospira lamellifera*, EPR, 13°N, diameter 0.94 mm.

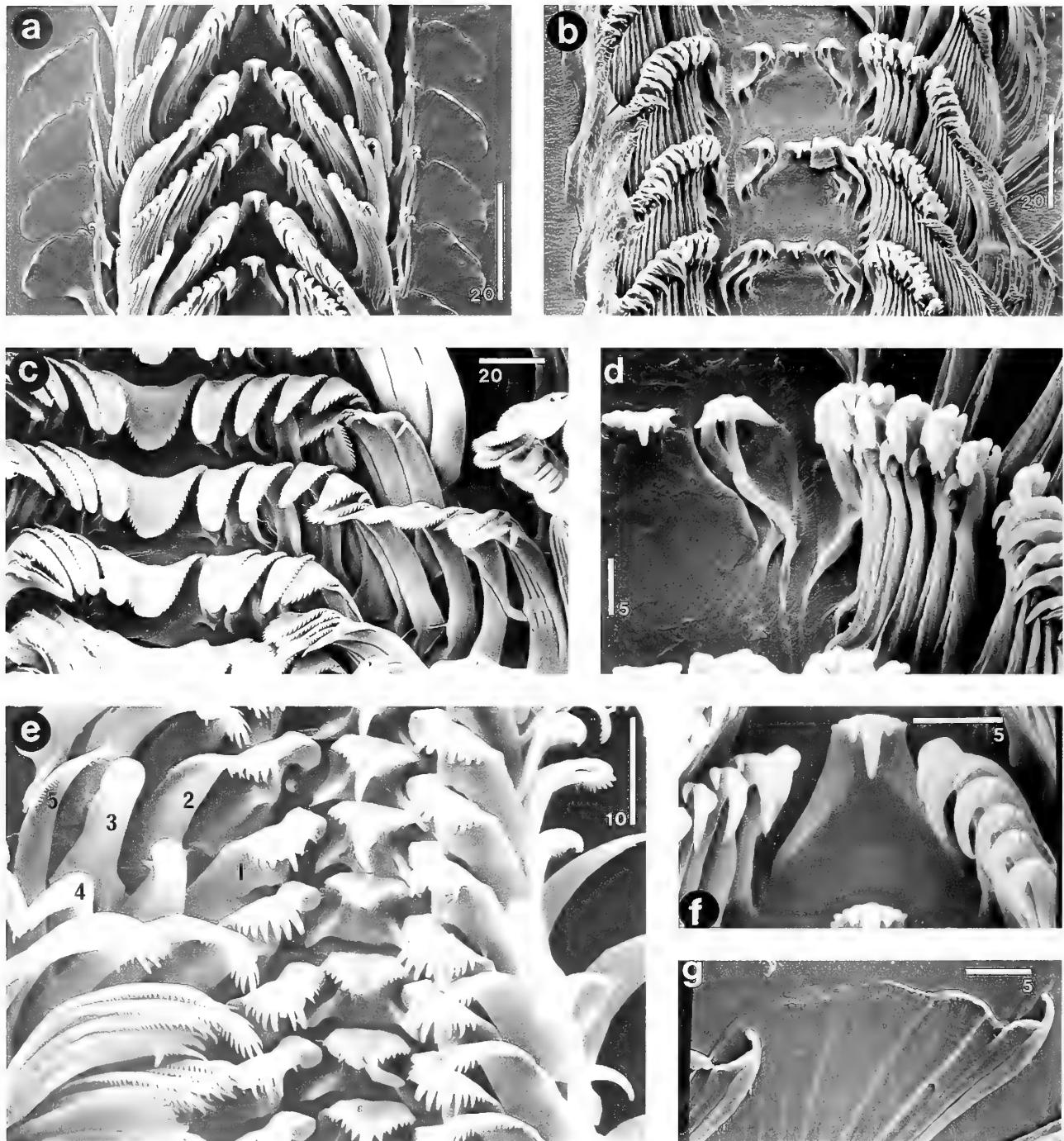


Figure 18. Radulae. Numbers indicate sequential order of teeth with central tooth as 0. a, f. *Sutilizona pterodon* Warén & Bouchet, sp. nov., MAR, Lucky Strike. f. Detail of central tooth. b, d, g. *S. tunnicliffae* Warén & Bouchet, sp. nov., holotype. b. Whole width. d. Detail of central field g. Detail of outer marginals. c. *Pseudorimula midatlantica*, MAR, Lucky Strike. e. *Retiskenea diploura* Warén & Bouchet, gen. & sp. nov., Aleutian Seeps, Shumagin site. Scale bars in µm.

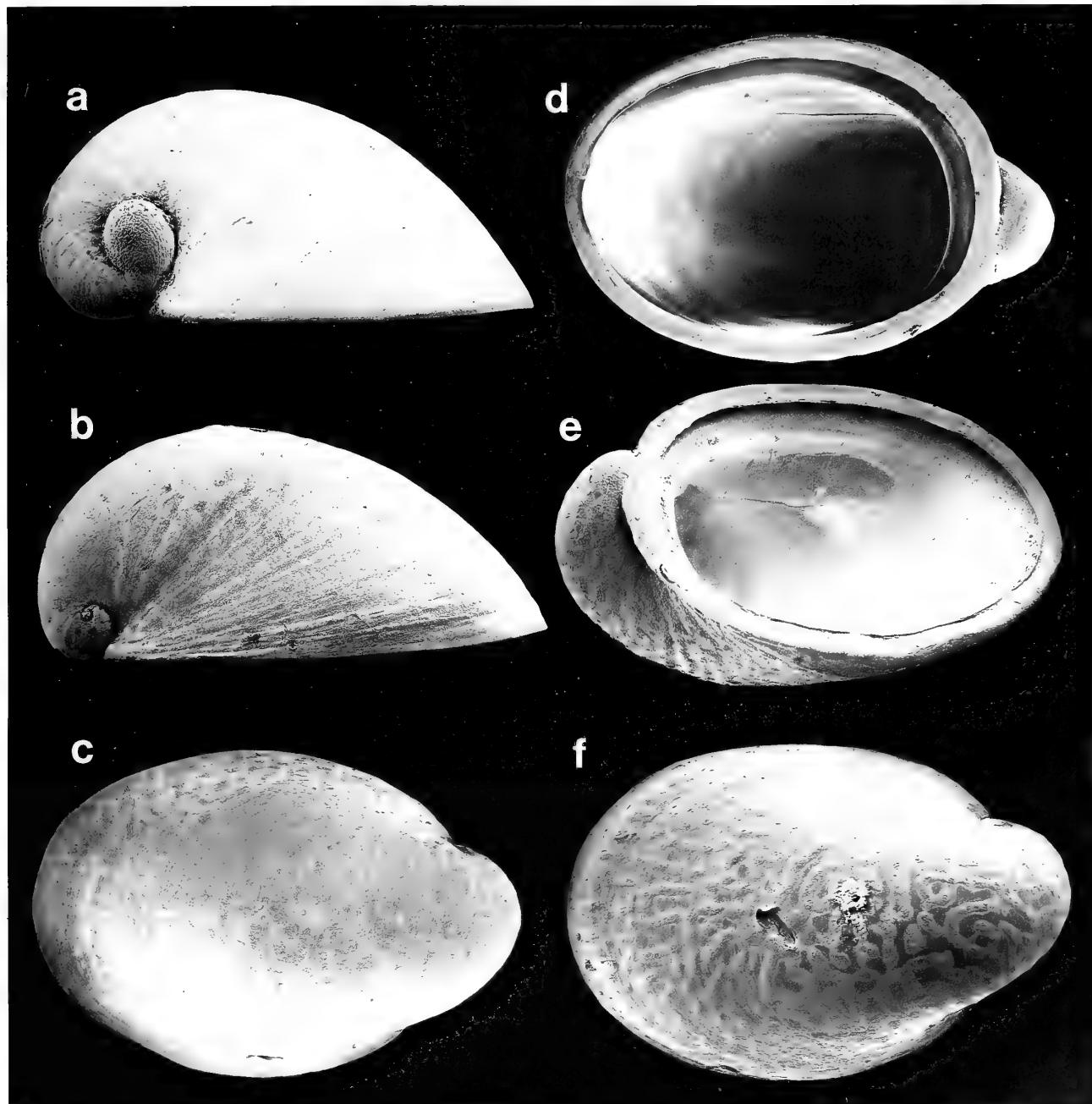


Figure 19. *Lepetodrilus atlanticus* Warén & Bouchet, sp. nov., MAR, Menez Gwen. *a*. Young specimen, 1.0 mm diameter. *b*. Adult, apical view, 5.9 mm diameter. *c*. Apical view, weakly patterned specimen, 5.7 mm diameter. *d*. Interior, diameter 6.0 mm. *e*. Oblique view of interior, diameter 6.7 mm. *f*. Strongly patterned specimen, diameter 3.4 mm.

sumed to be sensory. The gill is monopectinate and only the efferent axis developed. The leaflets are 0.7 mm wide and 1.3 mm high in a large specimen, slightly more than 50 in number. There is one major afferent vessel, transversing the most posterior part of the pallial skirt, from the rectum toward the gill, where it makes a 90° turn anteriorly, and numerous vessels in the hypobranchial

gland, which seem to join the leaflets. The rectum is inconspicuous, very thin, usually empty and flat. To the right of the rectum and fused to it is the pallial part of the gonoduct. The male one is much larger than the female one and reaches up to $\frac{1}{3}$ of its length in front of the rectum. The female one parallels $\frac{2}{3}$ of the rectum and is inconspicuous. Farther to the right is a low ridge which

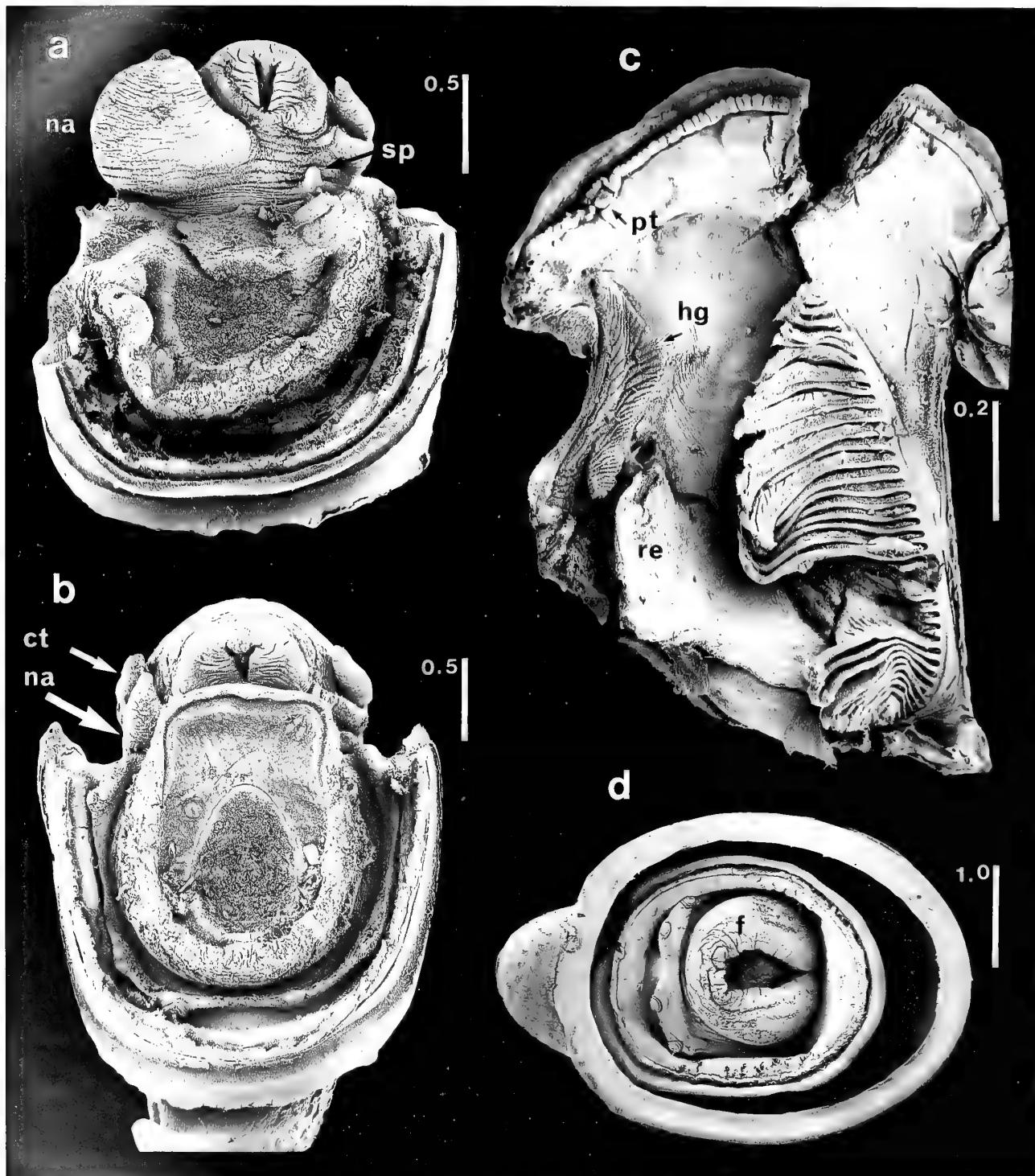


Figure 20. *Lepetodrilus atlanticus* Warén & Bouchet, sp. nov., critical-point dried, MAR, Menez Gwen. a. Male, anterior part of foot removed. b. Female. c. Pallial skirt; some central leaflets of gill removed. d. Animal in shell; normal contraction. ct - cephalic tentacle; f - foot; hg - hypobranchial gland; na - neck appendage; pt - pallial tentacle; re - rectum; sp - sensory papilla. Scale bars in mm.

seems to leave the most posterior part of the gonoduct and cross the pallial skirt to the thickened margin, dorsal to the sensory papilla. It contains a large blood vessel. The posterior part of this ridge has a comblike appearance from numerous small ridges formed by the hypobranchial gland and leaving it at approximately right angle, toward the gonoduct-rectal complex.

Radula (Figures 21a, b). n - 5 - 1 - 5 - n. As described for the genus but the central tooth is very low and sturdy. The first lateral tooth has an evenly serrated, narrow apical plate. The marginals start as rather sturdy, tall teeth with interlocking shafts and serrated, triangular, anteriorly directed apical plate. After about six to seven of these, they gradually transform into tall, narrow, tightly stacked laminar structures with the simple, serrated, ovate apical plate directed 45° from the longitudinal axis of the radula (and the shaft) by a subapical flexure of the shaft. The outer side of the shaft has a conspicuous spine at the base of the plate.

Remarks: About 40 specimens from Menez Gwen and Lucky Strike were sexed by light staining with karm alum, which accentuates the external appearance of the gonad; long acicular lobes in the male; granular in females. No questionable specimens were found, and although the males often are smaller, 0.5–0.7 of the size of the females, there is no indication of protandrous hermaphroditism, and the largest specimen of *L. atlanticus* (7.2 mm) was a male.

It is quite noticeable that *L. atlanticus* contracts more firmly when preserved than other species of the genus (Figure 20d). The contents of the gut consist of a mixture of sediment and organic material, possibly of planktonic origin.

Lepetodrilus cristatus McLean, 1988

(Figure 22a)

Lepetodrilus cristatus McLean, 1988: 15, figs. 13, 14, 57–65.

Lepetodrilus cristatus: Fretter, 1988: 53, figs. 11–12.

New records: EPR at 13°N: - HERO 91 PL 04, 34 spms; - HERO 91 PL 05, 2 spms; - HERO 91 PL 12, 3 spms; - HERO 91 PL 13, 35 spms; - HERO 91 PL 17, 3 spms; - HERO 91 PL 19, 1 spm; - HERO 91 PL 21, 1 spm; - HERO 91 PL 22, 1 spm; - HERO 91 PL 23, 1 spm; - HERO 91 PL 25, 4 spms; - HERO 92 dive 2514, 4 spms; - HERO 92 dive 2516, 3 spms; - HERO 92 dive 2517, 7 spms; - HERO 92 dive 2520, 1 spm; - HERO 92 dive 2521, 3 spms; - HERO 92 dive 2522, 22 spms; - HERO 92 dive 2523, 10 spms; - HERO 92 dive 2524, 1 spm; - HERO 92 dive 2528, 1 spm; - HERO 92 dive 2531, 2 spms.

Distribution: EPR at 21°N and 13°N, and the Galapagos Rift in 2500–2600 m depth.

Remarks: Almost all specimens were obtained from the retrieval box after recovery of tubes of Vestimentifera.

Lepetodrilus elevatus McLean, 1988

(Figure 22c)

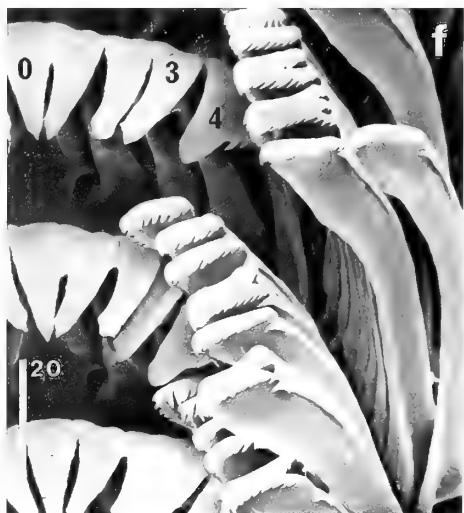
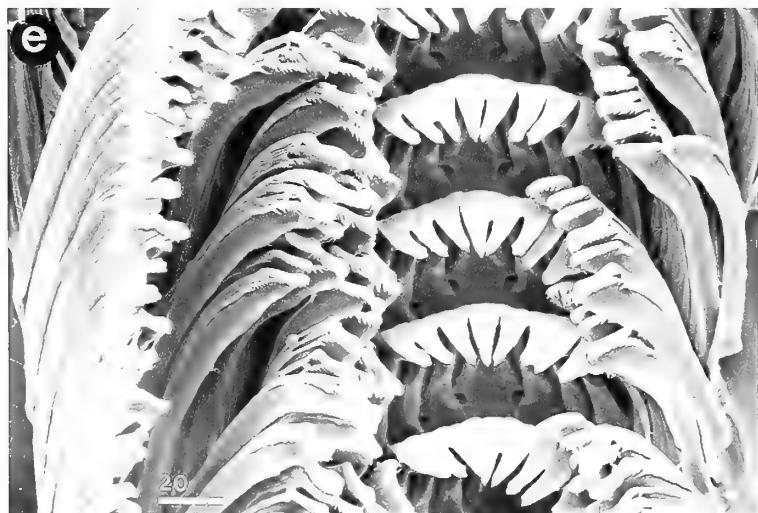
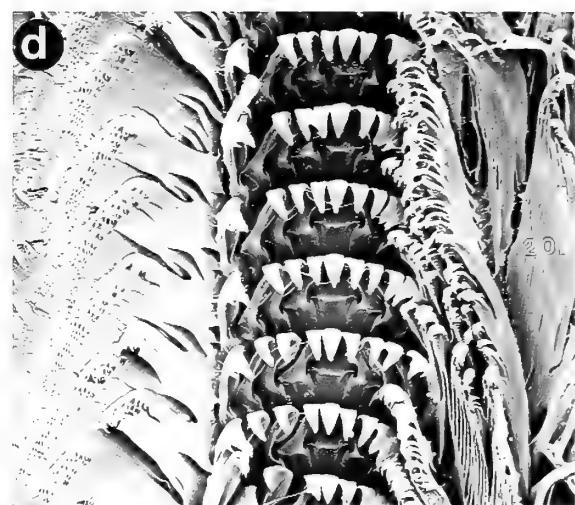
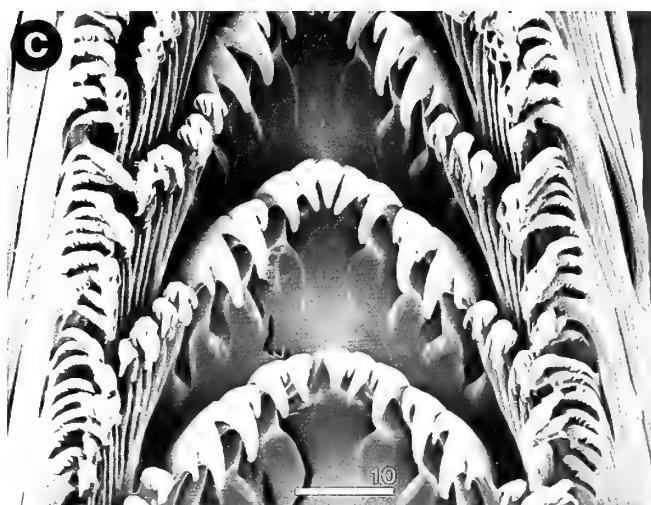
Lepetodrilus elevatus McLean, 1988: 11, figs. 5, 6, 36–44.

Lepetodrilus elevatus: Fretter, 1988: 49, figs. 7–8; McLean 1993: 32, figs. 17–25; Beck, 1993: 175.

New records: EPR at 13°N: - HERO 91 PL 09, 7 spms; - HERO 91 PL 10, 5526 spms; Genesis, 201 spms; - HERO 91 PL 11 (Genesis), 175 spms; - HERO 91 PL 12, 8900 spms; - HERO 91 PL 13 (Elsa), 3462 spms; - HERO 91 PL 17, 12063 spms; - HERO 91 PL 19, 1250 spms; - HERO 91 PL 21, 11773 spms; - HERO 91 PL 23, 4025 spms; - HERO 91 PL 24 (Elsa), 79 spms; - HERO 91 PL 25, 23 spms; - HERO 91 PL 26, 17000 spms; - HERO 91 PL 27, 20 spms; - HERO 92 dive 2512, 12440 spms; - HERO 92 dive 2514, 7340 spms; - HERO 92 dive 2516, 4440 spms; - HERO 92 dive 2517, 9968 spms; - HERO 92 dive 2519, 1800 spms; - HERO 92 dive 2520, 7100 spms; - HERO 92 dive 2521, 6290 spms; - HERO 92 dive 2522, 4050 spms; - HERO 92 dive 2523, 6370 spms; - HERO 92 dive 2524, 3000 spms; - HERO 92 dive 2525, 9700 spms; - HERO 92 dive 2526, 6700 spms; - HERO 92 dive 2528, 6900 spms; - HERO 92 dive 2531, 12840 spms; - HERO 92 dive 2532, 6830 spms. EPR at 09°50'N: - HERO 91 PL 09, 1 spm. EPR at 17°S: - NAUDUR PL 06, site Rehu, 50 spms; - NAUDUR PL 12 (Animal Farm), 1 spm; - NAUDUR PL 18 (Le Chat), 3 spms; - NAUDUR PL 18, site Rehu, 11 spms.

Distribution: Uncertain, see below. It does, however, seem certain that *L. elevatus* follows the EPR from 21°N to 17°S and also is present at the Galapagos rift (subspecies *galrifensis* McLean, 1988), at a depth of 2400–2700 m. Almost all specimens above come from tubes of Vestimentifera.

Remarks: McLean (1993) recorded *L. elevatus* from the Mariana Trough and noticed that a penis was absent. Warén & Bouchet (1993) recorded it from the North Fiji and Lau Basins. Beck (1993) found that none of 38 specimens from the Mariana Trough had a penis and questioned these identifications. We examined some 25 males from the North Fiji Basin (YOKOSUKA material) and found that most lack a penis, although scattered specimens have it well developed and several have more than the trace that is present in females. Beck (1993, in press) discussed the possibility of periodic reproduction and corresponding development of the penis, but at present there is no information to support this because we found that the gonads of the YOKOSUKA males were full and contained mature sperm also in specimens lacking a penis. These details, however, make the records from the western Pacific unreliable, and although we tentatively reidentify



them as *L. schrolli*, they should not be used for zoogeographic and similar discussions. The specimens from the EPR at 17°S do have a penis. Based on genetical distances, Craddock et al. (1997) hypothesized a low dispersal between populations of *L. elevatus* from the EPR.

It is also worth noticing that the proportions between the sexes vary considerably from one site to another (44–65% females in three samples of about 150 specimens each from three adjacent localities at EPR, 13°N). The gonad and male reproductive organ seem to become functional at a size between 2.5 and 3 mm. Also the size is somewhat variable. HERO 91 PL 13 hit a spot with an average size of 9–10 mm and a maximum size of 12.5 mm, while an average size of 5.5 mm and a maximum size of 6–7 mm is normal. The soft parts of these larger specimens agreed perfectly with those from other localities (outer part of gill bipectinate; penis present; sensory neck tubercle present).

The huge quantities of *L. elevatus* were obtained from vestimentiferan tubes, which are the main habitat of *L. elevatus*.

Lepetodrilus guaymasensis McLean 1988

Lepetodrilus guaymasensis McLean, 1988:16, figs. 15, 16, 66–74.

Lepetodrilus guaymasensis: Fretter, 1988:54, figs. 13–14.

New records: *Guaymas Basin*: - GUAYANAUT PL 07, 5 spms; - GUAYANAUT PL 15, 1 spm; - GUAYANAUT PL 17, 1 spm.

Distribution: Only known from the Gulf of California, Guaymas Basin, at about 2000 m depth.

Remarks: Fretter (1988:fig. 13) mentioned a pair of small post-tentacular appendages at the left side of the neck of males in this species. We have not been able to find them.

Lepetodrilus ovalis McLean, 1988

(Figure 22b)

Lepetodrilus ovalis McLean, 1988:14, figs. 9–12, 51–56.

Lepetodrilus ovalis: Fretter, 1988:50, figs. 8–10.

New records: EPR at 13°N: - HERO 91 PL 11 (Genesis), 3 spms; - HERO 91 PL 12, 1 spm; - HERO 91 PL 17, 1 spm; - HERO 91 PL 26, 1 spm; - HERO 92 dive 2517, 22 spms; - HERO 92 dive 2519, 1 spm; - HERO 92 dive 2523, 1 spm; - HERO 92 dive 2528, 22 spms; - HERO 92 dive 2531, 1 spm; - HERO 92 dive 2532, 2 spms.

EPR at 09°50'N: - HERO 91 PL 09, 21 spms. EPR at 17°S: - NAUDUR PL 06, Rehu, 111 spms; on mussels, 6 spms.

Distribution: EPR from 21°N to 17°S, at ca. 2500–2600 m depth. The specimens above were recovered from tubes of vestimentifera and from mussels.

Remarks: This species can be recognized by the presence of a small “sensory” tubercle at the ventral, right side of the neck; not the left as in other species with such a tubercle.

Lepetodrilus pustulosus McLean, 1988

(Figures 22d–e)

Lepetodrilus pustulosus McLean, 1988:8, figs 1–4, 25–35.

Lepetodrilus pustulosus: Fretter, 1988:35, figs 1–6.

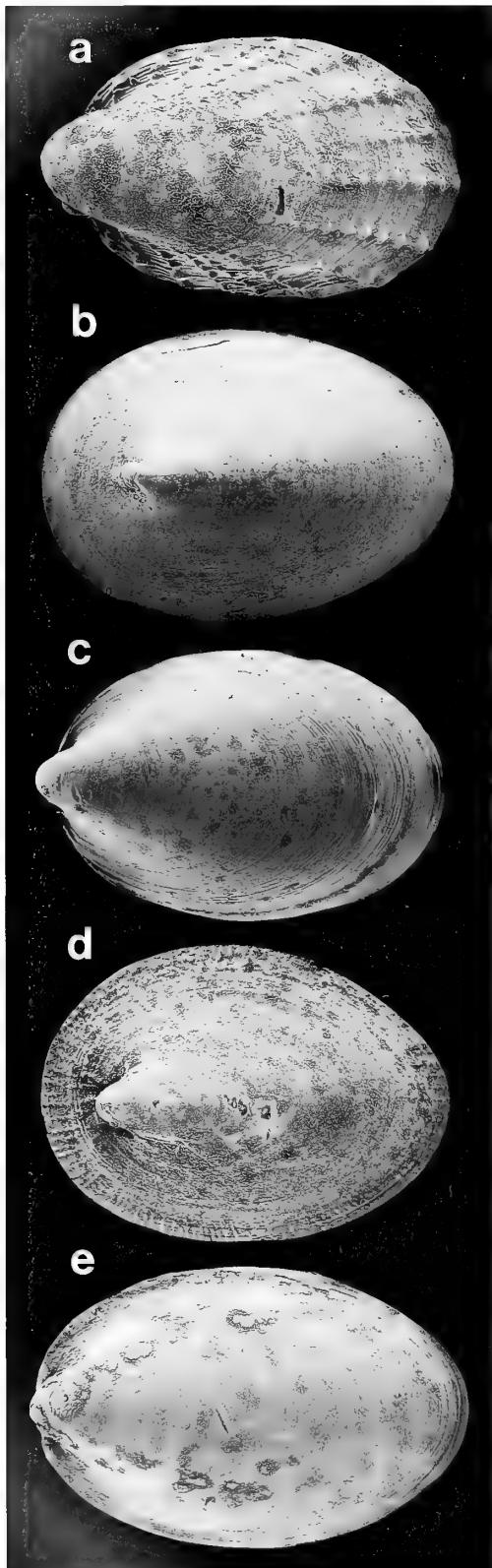
New records: EPR at 13°N: - HERO 91 PL 10 (Genesis), a few hundred spms; - HERO 91 PL 11 (Genesis), 10 spms; - HERO 91 PL 12, 12 spms; - HERO 91 PL 13, 37 spms; - HERO 91 PL 17, 103 spms; - HERO 91 PL 19, 41 spms; - HERO 91 PL 21, 276 spms; - HERO 91 PL 22, 137 spms; - HERO 91 PL 24 (Elsa), 3 spms; - HERO 91 PL 25, 2 spms; - HERO 91 PL 26, 81 spms; - HERO 91 PL 27, 3 spms; - HERO 92 dive 2512, 357 spms; - HERO 92 dive 2514, 233 spms; - HERO 92 dive 2516, 42 spms; - HERO 92 dive 2517, 188 spms; - HERO 92 dive 2519, 41 spms; - HERO 92 dive 2520, 104 spms; - HERO 92 dive 2521, 125 spms; - HERO 92 dive 2522, 14 spms; - HERO 92 dive 2523, 245 spms; - HERO 92 dive 2525, 232 spms; - HERO 92 dive 2526, 169 spms; - HERO 92 dive 2528, 93 spms; - HERO 92 dive 2531, 197 spms; - HERO 92 dive 2532, 168 spms. EPR at 17°S: - NAUDUR PL 06, site Rehu, 2 spms; - NAUDUR PL 18 (Gwen Meur), 2 spms; Le Chat, 8 spms; Rehu, 3 spms; - NAUDUR PL 04.8b, site Rehu, 10 spms.

Distribution: EPR from 21°N to 17°S, at about 2600 m depth. Most specimens were recovered from tubes of vestimentifera.

Remarks: Young specimens of *Lepetodrilus pustulosus* may be difficult to identify, because there is a considerable variation in shell shape. Up to a size of about 1 mm they are short and broad with a distinct spire and resemble *Gorgoleptis spiralis*. Then they become more slender, up to 2–2.5 mm in length, but still the “spire” is touching the posterior shell margin. At this size the species resembles *L. elevatus*. At 2.5–3 mm in length the “spire” starts

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Figure 21. Radulae. a, b. Numbers indicate sequential order of teeth with central tooth as 0. *Lepetodrilus atlanticus* Warén & Bouchet, sp. nov., MAR, Menez Gwen. a. Half width. b. Detail of central and first lateral teeth. c. *Melanodrymia galeronae* Warén & Bouchet, sp. nov., paratype. d. *Melanodrymia* sp., “rust covered,” EPR, 13°N, Caldera. e, f. *Peltospira rigneae* Warén & Bouchet, sp. nov., holotype. e. Whole width. f. Detail of marginals. Scale bars in μm .



its relative movement toward the center of the shell, and in adult specimens its posterior margin is situated $\frac{1}{3}$ from the posterior shell margin. The pustulose sculpture starts its development at the same time as the change in shape starts. This ontogenetic change in shell shape varies between different localities, at some it starts earlier, at others later. The consequence of this is that in some cases different populations have the "spire" situated more or less close to the posterior margin when specimens of the same size are compared (Figures 22d–e.) The shape of the shell closely resembles young specimens of *L. ovalis* (Figure 22b), but that species has a perfectly smooth shell at a size of 2–4 mm, when there is risk for confusion. *Lepetodrilus cristatus* is easy to separate because of its much stronger sculpture (Figure 22a). Based on genetical distances, Craddock et al. (1997) hypothesized a high dispersal between populations of *L. pustulosus* from the EPR.

Lepetodrilus fucensis McLean, 1988

Lepetodrilus fucensis McLean, 1988:18, figs. 17–20, 75–83.

New records: JdF, Axial Seamount: - ROPOS 406, 10 spms (FMNH 280890).

Distribution: Most localities investigated at the JdF, ca. 1500–2200 m.

Remarks: The basal plane of the shell of *L. fucensis* is more irregular than in any other species of the genus, probably indicating a more sedentary life.

Gorgoleptis McLean, 1988

Gorgoleptis McLean, 1988:19.

Type species: *G. emarginatus* McLean, 1988; by original designation; hydrothermal vents at the EPR.

Remarks: All species of *Gorgoleptis* keep the operculum until just below the maximum size. The species are usually rare, much more so than the species of *Lepetodrilus*. We figure shells of *G. emarginatus* and *G. spiralis* to supplement McLean's figures; our single specimen of *G. patulus* is too poor for figuring.

Gorgoleptis emarginatus McLean, 1988

(Figure 17b)

Gorgoleptis emarginatus McLean, 1988:22, figs. 21–24, 84–92.

←

Figure 22. *Lepetodrilus* spp. young specimens a. *L. cristatus*, EPR, 13°N, 1.9 mm. b. *L. ovalis*, EPR, 13°N, 2.4 mm. c. *L. elevatus*, EPR, 13°N, 2.6 mm. d. *L. pustulosus*, EPR, 13°N, 3.2 mm. e. *L. pustulosus*, EPR, 13°N, 2.9 mm. Notice the start of radial sculpture at the posterior end. The initiation of this sculpture coincides with the beginning displacement of the apex toward the center.

Gorgoleptis emarginatus: Fretter, 1988:58, figs. 16–17.

New records: EPR at 13°N: - HERO 91 PL 10, 2 spms; - HERO 91 PL 11 (Genesis), 2 spms; - HERO 92 dive 2517, 2 spms; - HERO 92 dive 2528, 1 spm.

Distribution: EPR at 21°N to 09°50'N, about 2600 m depth, mostly from vestimentiferan tubes.

Remarks: *Gorgoleptis emarginatus* was earlier known only from 21°N. Typical features are the slender and evenly tapering labial penis, flat and broad shell, and narrow periostracal strip at the columella.

The larva of *Gorgoleptis* sp. was identified in plankton samples taken a few meters above the sea floor at the EPR at 09°50'N (Mullineaux et al., 1996).

Gorgoleptis spiralis McLean, 1988

(Figure 17a)

Gorgoleptis spiralis McLean, 1988:23, figs. 93–97.

Gorgoleptis spiralis: Fretter, 1988:64, fig. 18b–c.

New records: EPR at 13°N: - HERO 91 PL 19, 1 spm; - HERO 92 dive 2517, 44 spms; - HERO 92 dive 2523, 1 spm; - HERO 92 dive 2526, 1 spm; - HERO 92 dive 2528, 14 spms.

Distribution: EPR at 13°N, ca. 2630 m, from vestimentiferan tubes.

Remarks: This species was described from three specimens in not very good condition. The maximum size in our material is 4.4 mm. A good character to recognize males of this species is the penis which is not evenly tapering as in *G. emarginatus* but ends in an uneven bifurcation with a larger, urn-shaped limb (Warén, in press: fig. 7b, d). The shell is almost smooth, with some indistinct indications of spiral lines.

Gorgoleptis patulus McLean, 1988

Gorgoleptis patulus McLean, 1988:24, figs. 98–102.

Gorgoleptis patulus: Fretter, 1988:65, figs. 18b, c; Warén in press.

New records: EPR at 13°N: - HERO 91 PL 19, 1 spm, from tubes of vestimentifera.

Distribution: EPR at 13°N, ca. 2600 m depth.

Remarks: The specimen is not in good condition and the identification is tentative. It does however have the narrow strip of periostracum at the rear end of the body, not a semicircular zone as in *G. spiralis*, although the shell is more similar to this species than to *G. emarginatus*. The length of the shell is 4.6 mm, considerably larger than the two specimens on which the name was founded (2.8 mm).

Clypeosectus McLean, 1989

Clypeosectus McLean, 1989:17.

Type species: *C. delectus* McLean, 1989; by original designation; hydrothermal vents at the Galapagos Rift.

Clypeosectus delectus McLean, 1989

Clypeosectus delectus McLean, 1989a:18, figs. 7A–H, 8A–H, 9A–F, 11A–E.

Clypeosectus delectus: Haszprunar, 1989b:5, fig. 4; Warén, in press.

New records: EPR at 13°N: - HERO 92 dive 2516, 2 spms; - HERO 92 dive 2521, 1 spm; - HERO 92 dive 2523, 1 spm; - HERO 92 dive 2528, 1 spm; - HERO 92 dive 2532, 1 spm. EPR at 17°S: - NAUDUR PL 06, site Rehu, 6 spms.

Distribution: EPR from 21°N to 17°S and the Galapagos Rift, ca. 2400–2600 m from vestimentiferan tubes.

Remarks: The larva of *Clypeosectus delectus* was identified in plankton samples taken a few meters above the sea floor at the EPR at 09°50'N (Mullineaux et al., 1996).

Clypeosectus curvus McLean, 1989

Clypeosectus curvus McLean, 1989a:21, figs. 10A–H, 11F.

New records: JdF, Axial Seamount, Ashes vent field: - ROPOS R406, 2 spms (FMNH 280887).

Distribution: JdF, 1500–2200 m depth.

Pseudorimula McLean, 1989

Pseudorimula McLean, 1989a:22.

Type species: *P. mariana* McLean, 1989; by original designation; vents at the Mariana Back Arc Basin.

Remarks: There are two known (and one undescribed, Beck, personal communication) species of the genus, both of a fairly uniform shell morphology. The main difference between *P. mariana* and *P. midatlantica* is that the right part of the shell muscle forms a single entity of even thickness in the latter, while it is divided in two main parts in *P. mariana*.

Pseudorimula midatlantica McLean, 1992

(Figures 15h, 18c, 23a–h)

Pseudorimula midatlantica McLean, 1992a:116, figs. 1–7.

Pseudorimula midatlantica: Warén, in press.

New records: MAR, Lucky Strike: - DIVA 1 PL 09, 1 spm; - DIVA 1 PL 19, among mussels, 2 spms; - DIVA 2 PL 01, 9 spms; - DIVA 2 PL 02, 2 spms; - DIVA 2 PL 04, 3 spms; - DIVA 2 PL 05, 5 spms; - DIVA 2 PL 07,

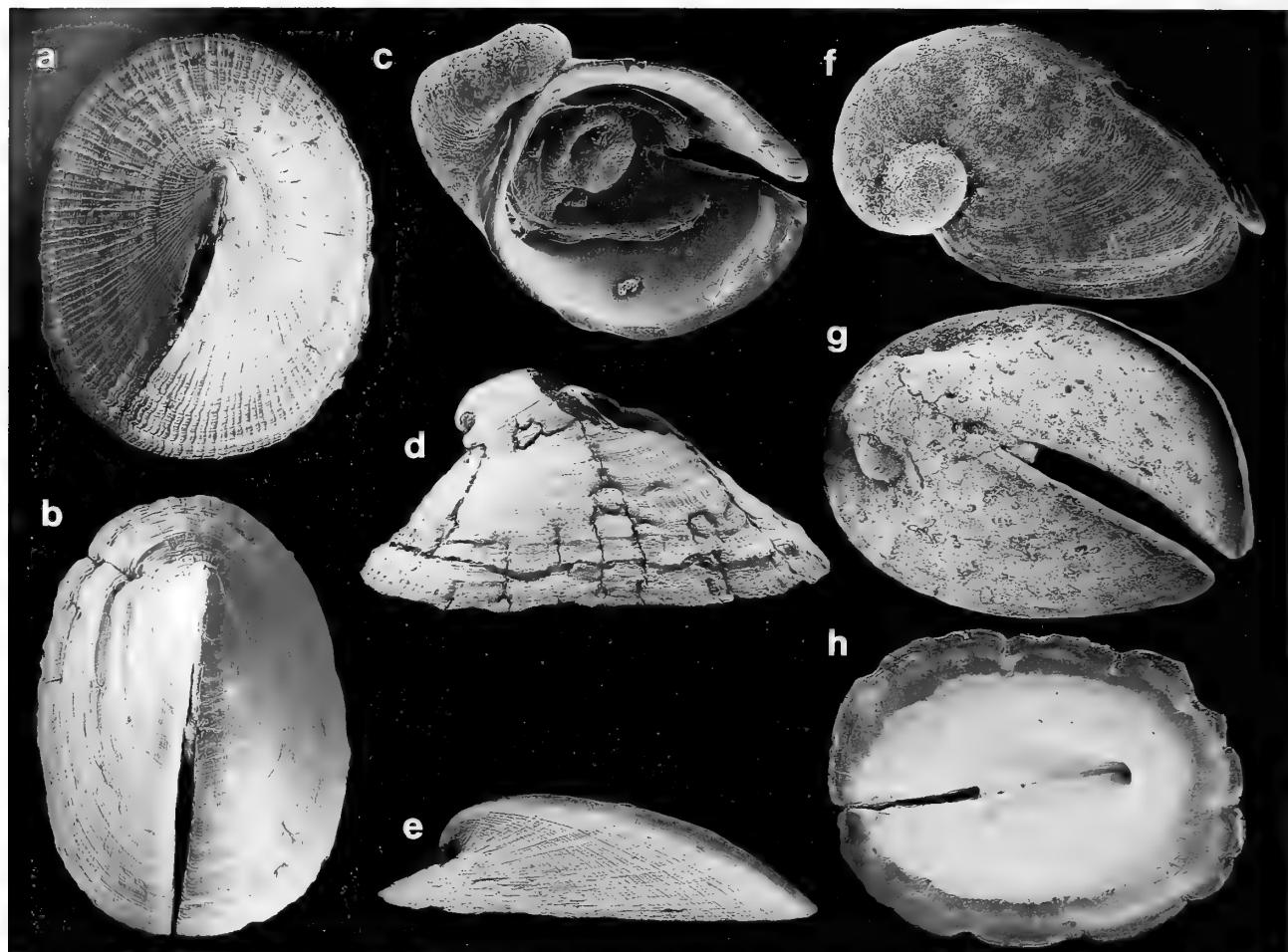


Figure 23. *Pseudorimula midatlantica*, MAR, shell morphology. a. Menez Gwen, diameter 6.6 mm. b. Lucky Strike, diameter 6.3 mm. c. Young specimen, Lucky Strike, diameter 0.75 mm. d. Cleaned shell, damaged by corrosion and repaired, apical part of slit enlarged, Lucky Strike, diameter 4.9 mm. e. Unusually flat specimen, Lucky Strike, diameter 8.4 mm. f. Young specimen, Lucky Strike, diameter 2.4 mm. g. Half grown specimen, not cleaned, Lucky Strike, diameter 0.7 mm. h. Inside, Lucky Strike, diameter 7.7 mm.

1 young; - DIVA 2 PL 10, on a rock, 1 spm; in retrieval box, 1 spm; - DIVA 2 PL 20, 9 spms; - DIVA 2 PL 21, 1 spm; - DIVA 2 PL 24, 5 spms; - LUSTRE Exp. Tour Eiffel, on mussels, 5 spms; - Sintra site, on mussels, 2 spms; - MARVEL PL1191, Bairro Alto, retrieval box, 1 spm; - MARVEL PL1192, Bairro Alto, retrieval box, 1630 m, 2 spms; - MARVEL PL1193, Tour Eiffel, retrieval box, 1 spm; on *Bathymodiolus*, 3 shs; - MARVEL PL1200, Bairro Alto, 0.25 m² rock surface close to edifice, 5 spms; - MARVEL PL1205, Bairro Alto, retrieval box, 2 spms. *Snake Pit*: - ALVIN dive 2613, 11 spms; - ALVIN dive 2614, 38 spms; - ALVIN dive 2615, 1 spm; - ALVIN dive 2617, 64 spms; - ALVIN dive 2619, 55 spms; - ALVIN dive 2621, 19 spms; - ALVIN dive 2622, 2 spms; - MICROSMOKE PL 07, 1 spm. *Logatchev site*: - MICROSMOKE PL 20, 1 spm.

Distribution: The MAR from 38°N to 14°45'N, in 1500–

3500 m depth. *Pseudorimula midatlantica* lives on rocks and mussels.

Remarks: *Pseudorimula midatlantica* is highly variable in shape and sculpture, from large, flat, almost smooth specimens (Figures 23b, e) to smaller and taller specimens with more pronounced sculpture (Figure 23d). We have, however, not been able to distinguish more than one species. When McLean (1992a) described the species, only a single well preserved shell was available, and we have illustrated additional specimens to show the variation. The protoconch (Figure 15h) is of normal appearance for Lepetodriloidae and of a diameter of about 215 µm.

The shell is frequently covered by thick crusts of bacterially precipitated iron and manganese oxides which obviously form an obstacle for the water circulation since frequently only a narrow hole remains open (Warén, in

press, fig. 1E). This causes a reaction from the snail which tries to widen the outlet, from the long, narrow slit typical for specimens with no rust cover, to a wide irregular opening (Figure 23d).

Warén (in press) described many details in the ontogeny and morphology of this species.

The food consists of a mixture of mineral particles and organic material scraped off from the surface of the rocks and shells it lives on.

Subclass Uncertain

Superfamily NEOMPHALOIDEA McLean, 1981

Remarks: The systematic position of Neomphaloidea ("Hot Vent Taxa" sensu Ponder & Lindberg, 1997) was considered somewhat uncertain by these authors, and their analysis indicated paraphyly. On the other hand, monophyly of Peltospiroidea and Neomphaloidea was supported by molecular information (McArthur, 1996; McArthur & Tunnicliffe, 1998). Ongoing anatomical work (Israelsson, 1998, in press) on several species of Neomphalidae, Cyathermiidae and Melanodrymiidae is producing evidence that the species of these families are quite closely related, and we place them together under Neomphalidae. They share, in addition to similarities in internal anatomy, the type of protoconch sculpture and a tendency to specialization of the left cephalic tentacle as a copulatory organ.

We have also moved *Planorbidella* and *Pachydermia* from Peltospiridae to Neomphalidae, since they have the same type of protoconch as *Neomphalus*. A result of our view is that the concept Neomphaloidea becomes synonymous with Neomphalina.

Family NEOMPHALIDAE McLean, 1981

Retiskenea Warén & Bouchet, gen. nov.

Type species: *Retiskenea diploura*, sp. nov.

Diagnosis: Shell small, globular, transparent, narrowly umbilicate with exquisite net sculpture on protoconch. Cephalic tentacles joined by a skin fold across the snout, laterally ciliated, possibly also with some additional skin folds between tentacles, left one probably with a basal penial process in adult males. No sensory papillae. Snout slightly flattened, distally broader. Foot broad, flat, and rounded, anteriorly drawn out to small corner tentacles, posteriorly broadly rounded and notched. Single epipodial tentacle at each side of anterior part of operculum. Gill small, centrally situated in pallial cavity, bipectinate. Stomach very large, intestine with single, simple anterior loop in head-foot, then a posterior loop to the right of stomach before entering pallial cavity. Conspicuous seminal vesicle at right side behind pallial cavity. Two large salivary glands open into the buccal cavity via short ducts. Jaw yellowish, present, not examined in detail.

Radula n - 1 - 1 - 1 - n, about four times as long as broad. Radular sac bilobed. Central tooth rather low, with antero-lateral supports and posterior, winglike projections, together forming a support for the first lateral tooth. Lateral tooth rather short and broad; marginals gradually more oarlike toward edge of radula. Operculum multispiral, with central nucleus, width of last whorl corresponds to 20% of diameter.

Etymology: From "rete" (Latin), net and "*Skenea*," a genus of gastropods of similar shell shape.

Remarks: We have made a new genus for this little species because of the strange combination of posteriorly bifurcated foot, ciliated snout and tentacles (heterobranch characters), and a protoconch, epipodial tentacle, and radula with bilobed sac, which are more traditional vetigastropod features. The radula is also quite similar to some species of Seguenziidae. The sculpture of the protoconch closely resembles the type found in Neomphalidae; a slight difference is that the ridges that form the net are of a fairly uniform size, while in the neomphalids their strength is more variable. The shape of the central tooth comes close to several species of *Ancistrobasis* (Marshall, 1991:fig. 271) or *Vetulonia* (Warén & Bouchet, 1993:figs 8B-C), species classified in Seguenziidae and Calliotropinae respectively. The lateral tooth, at the same time as it is similar to that of these genera, also resembles that of *Halogyrina*, but is more sturdy.

Four specimens of a size between 1.3 and 1.5 mm were critical-point dried but with meager results. The specimens were poorly preserved, except one which was badly covered by mucus. That specimen showed some signs of developing additional cephalic appendages not present in the others. That one was also the largest specimen with soft parts, diameter 1.5 mm, while a couple of almost fossilized shells had a diameter of 2.2 mm. This indicates that our specimens were immature, and perhaps, had not yet developed the tentacular appendages. We have therefore figured a critical-point dried specimen of *Retiskenea* sp. from off Oregon, which we could not safely identify, since it was decalcified. The radula is, however, identical, the soft parts agree with what can be seen in our specimens of *R. diploura*, and the periostracum gave an idea of a very similar shape of the shell. It may, however, represent a second species.

It is not easy to classify this genus because of the strange combination of characters. We have placed *Retiskenea* in Neomphalidae because of presence of epipodial tentacles, similarity in protoconch sculpture, supposed dimorphism of cephalic tentacles, and strange plate between the cephalic tentacles, which closely resembles that in the male of *Melanodrymia*.

Depressigryra? statura Goedert & Benham, 1999, from Middle Eocene seep deposits in the state of Washington closely resembles *R. diploura* in the shape of the protoconch and teleoconch. The protoconch sculpture was well

enough preserved to allow examination, and is very similar (specimens through the courtesy of the authors). Another difference from *Depressigryra* is that the aperture is almost tangential, while it is clearly radial in *Depressigryra*. We therefore transfer *D. statura* to *Retiskenea*.

Retiskenea diploura Warén & Bouchet, sp. nov.

(Figures 15j, 16g, 18e, 24c)

Type material: Holotype SMF 311984 and 17 paratypes SMF 311985, 9 paratypes MNHN.

Type locality: Aleutian Trench, Shumagin site, TVGKG 40, 54°18.17'N, 157°11.82'W, 4808 m.

Material examined: The type material and: *Aleutian Trench*: - TVGKG 49, 2 specimens.

Distribution: Only known from the Aleutian Trench, Shumagin site at 4800 m.

Etymology: From “diplo,” double and “oura,” tail (Greek), referring to the posteriorly bifurcated foot.

Description: *Shell* (Figure 24c). Small, greyish semi-transparent with a very thin periostracum, of a tall skeletoconch shape. The protoconch (Figure 15j) consists of $\frac{2}{3}$ of a whorl, has a large initial part and is completely covered by fine ridges, forming a network with slightly variable mesh size, distinctly smaller toward the peristome. Its diameter is 300 μm . The teleoconch consists of up to three distinctly convex whorls, united by a deep suture and sculptured by irregularly spaced growth lines of variable strength. There is also a microsculpture of small pits, diameter 1–2 μm , evenly distributed over all the surface. The umbilicus is narrow and deep. The outer lip is thin and sharp, the peristome almost round, slightly indented by the preceding whorl.

Dimensions. Diameter of holotype 1.20 mm, height 1.34 mm, maximum diameter 2.2 mm (old shells only).

Operculum (Figure 16g) and **radula** (Figure 18e). See generic diagnosis.

Remarks: As mentioned above, it seems likely that our specimens are immature. This is also supported by the fact that the protoconchs were perfectly preserved in all live taken specimens, while in other species from the same locality and of similar size, it was completely lost.

***Retiskenea* sp.**

(Figures 25a–e)

Material examined: *Oregon Margin*: - ROPOS 341, suction sample 1, 1 decalcified specimen.

Remarks: A single completely decalcified specimen had the thin colorless periostracum remaining and showing

the shape of the shell. It was very similar to *R. diploura*, diameter ca. 2.4 mm, with 3.2 whorls left and no trace of the apex remaining. It was used for critical-point drying and radula preparation. We figure it since it gives a better idea about the soft parts of *Retiskenea* than our SEM photos of the type species.

Cyathermia Warén & Bouchet, 1989

Cyathermia Warén & Bouchet, 1989:69.

Type species: *C. naticoides* Warén & Bouchet, 1989; by original designation; hydrothermal vents at EPR.

Cyathermia naticoides Warén & Bouchet, 1989

Cyathermia naticoides Warén & Bouchet, 1989:70, figs. 6–10, 15, 16, 18, 21–23, 71, 80.

Cyathermia naticoides: Warén & Bouchet, 1993:33.

New records: EPR at 13°N: - HERO 91 PL 10, 900 spms; Genesis, 10 spms; - HERO 91 PL 11 (Genesis), 59 spms; - HERO 91 PL 12, 2 spms; - HERO 91 PL 13, 883 spms; - HERO 91 PL 17, 992 spms; - HERO 91 PL 19, 9 spms; - HERO 91 PL 21, 1565 spms; - HERO 91 PL 23 (Elsa), 131 spms; - HERO 91 PL 24 (Elsa), 5 spms; - HERO 91 PL 26, 140 spms; - HERO 92 dive 2512, 315 spms; - HERO 92 dive 2514, 970 spms; - HERO 92 dive 2516, 32 spms; - HERO 92 dive 2517, 6 spms; - HERO 92 dive 2519, 96 spms; - HERO 92 dive 2520, 713 spms; - HERO 92 dive 2521, 713 spms; - HERO 92 dive 2522, 147 spms; - HERO 92 dive 2523, 1400 spms; - HERO 92 dive 2524, 103 spms; - HERO 92 dive 2525, 1125 spms; - HERO 92 dive 2526, 129 spms; - HERO 92 dive 2528, 822 spms; - HERO 92 dive 2531, 822 spms; - HERO 92 dive 2532, 852 spms. EPR at 09°50'N: - HERO 91 PL 07, 7 spms; - HERO 91 PL 09, 2 spms.

Distribution: EPR between 09°50'N and 21°N, in about 2600 m depth. Almost all specimens come from tubes of vestimentifera.

Remarks: The anatomy is described by Israelsson (in press). It is there shown that the species is closely related to *Neomphalus*.

The larva of *C. naticoides* was identified in plankton samples taken a few meters above the sea floor at the EPR at 09°50'N (Mullineaux et al., 1996).

Melanodrymia Hickman, 1984

Melanodrymia Hickman, 1984:19.

Type species: *M. aurantiaca* Hickman, 1984; by original designation; hydrothermal vents at the Galapagos Rift Zone and the EPR.

Remarks: *Melanodrymia galeronae* may perhaps look very different from *M. aurantiaca*, but this is only the result of a slightly taller spire. Other details are quite

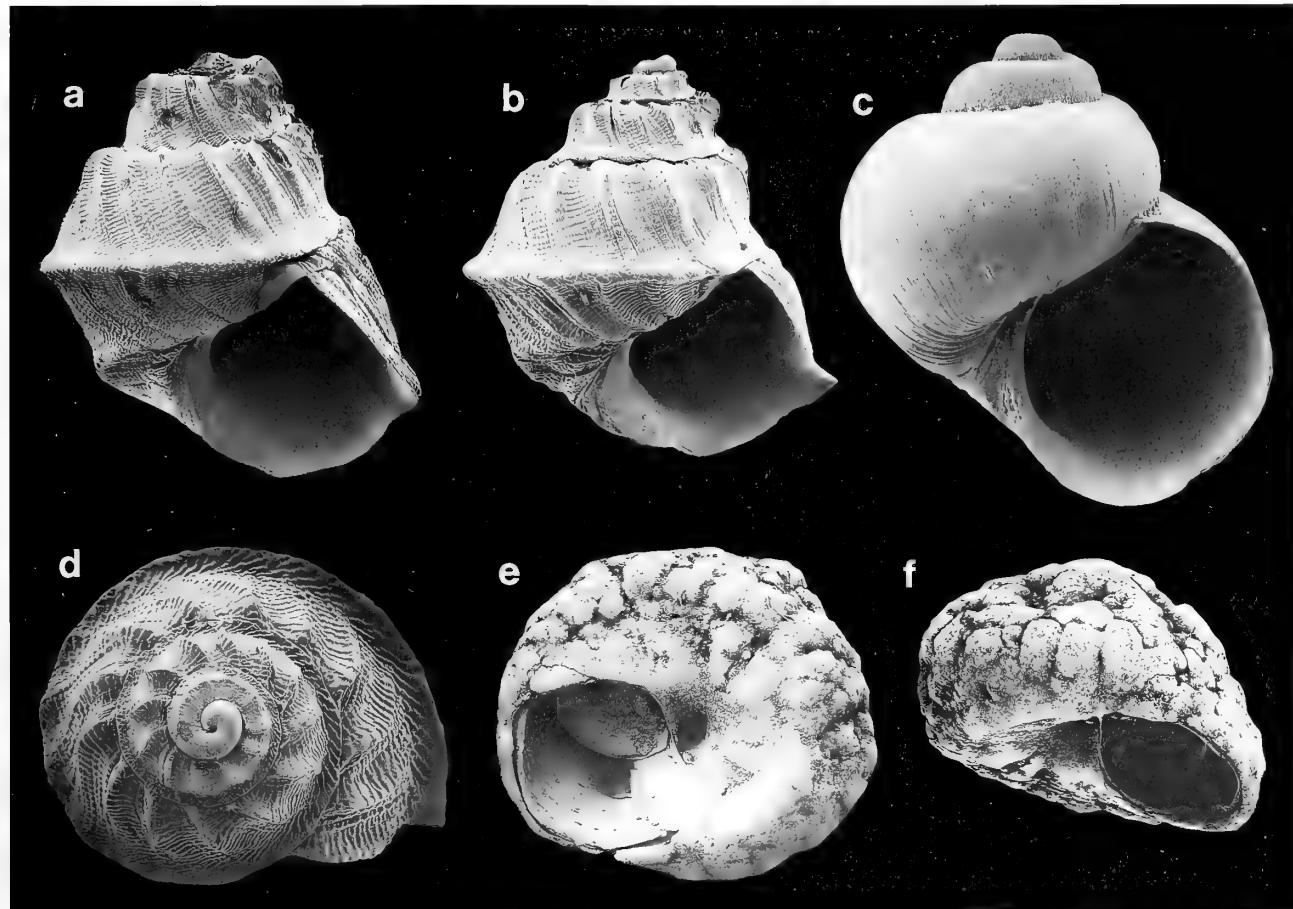


Figure 24. Neomphalidae, shells. *a, b, d*. *Melanodrymia galeronae* Warén & Bouchet, sp. nov., paratypes. *a*. Adult shell, 3.0 mm height. *b*. Subadult shell, 2.6 mm height. *d*. Apical view, diameter 1.74 mm. *c*. *Retiskenea diploura* Warén & Bouchet, gen. & sp. nov., paratype, diameter 1.34 mm. *e, f*. *Melanodrymia* sp., “rust covered”, EPR, 13°N, Caldera. *e*. Basal view, diameter 3.6 mm. *f*. Apertural view, diameter 3.2 mm.

similar to the type species, and the genus forms a morphologically rather narrow group.

Melanodrymia aurantiaca Hickman, 1984

Melanodrymia aurantiaca Hickman, 1984:20, figs. 1–2.
Melanodrymia aurantiaca: Haszprunar, 1989a:175; Warén & Bouchet, 1993:41; Israelsson, 1998:105.

New records: EPR at 13°N: - HERO 91 PL 10, 3 spms; - HERO 91 PL 11 (Genesis), 12 spms; - HERO 91 PL 19, 2 spms; - HERO 91 PL 25 (Caldera), 5 spms; - HERO 92 dive 2512, 1 spm; - HERO 92 dive 2522, 54 spms; - HERO 92 dive 2523, 8 spms. EPR at 17°S: - NAUDUR PL 03 (Nadir), 1 spm; - NAUDUR PL 04, site Rehu, 1 spm; - NAUDUR PL 06, site Rehu, 17 spms.

Distribution: EPR from 21°N to 17°S, in 2500–2600 m depth.

Remarks: The largest specimen has a shell diameter of 3.6 mm.

Melanodrymia brightae Warén & Bouchet, 1993

Melanodrymia brightae Warén & Bouchet, 1993:43, figs. 34A–C, 35A–B.

New records: JdF, Endeavour Segment: - ROPOS 278, from rocks, 37 spms (MNHN, Tunnicliffe ref. coll.).

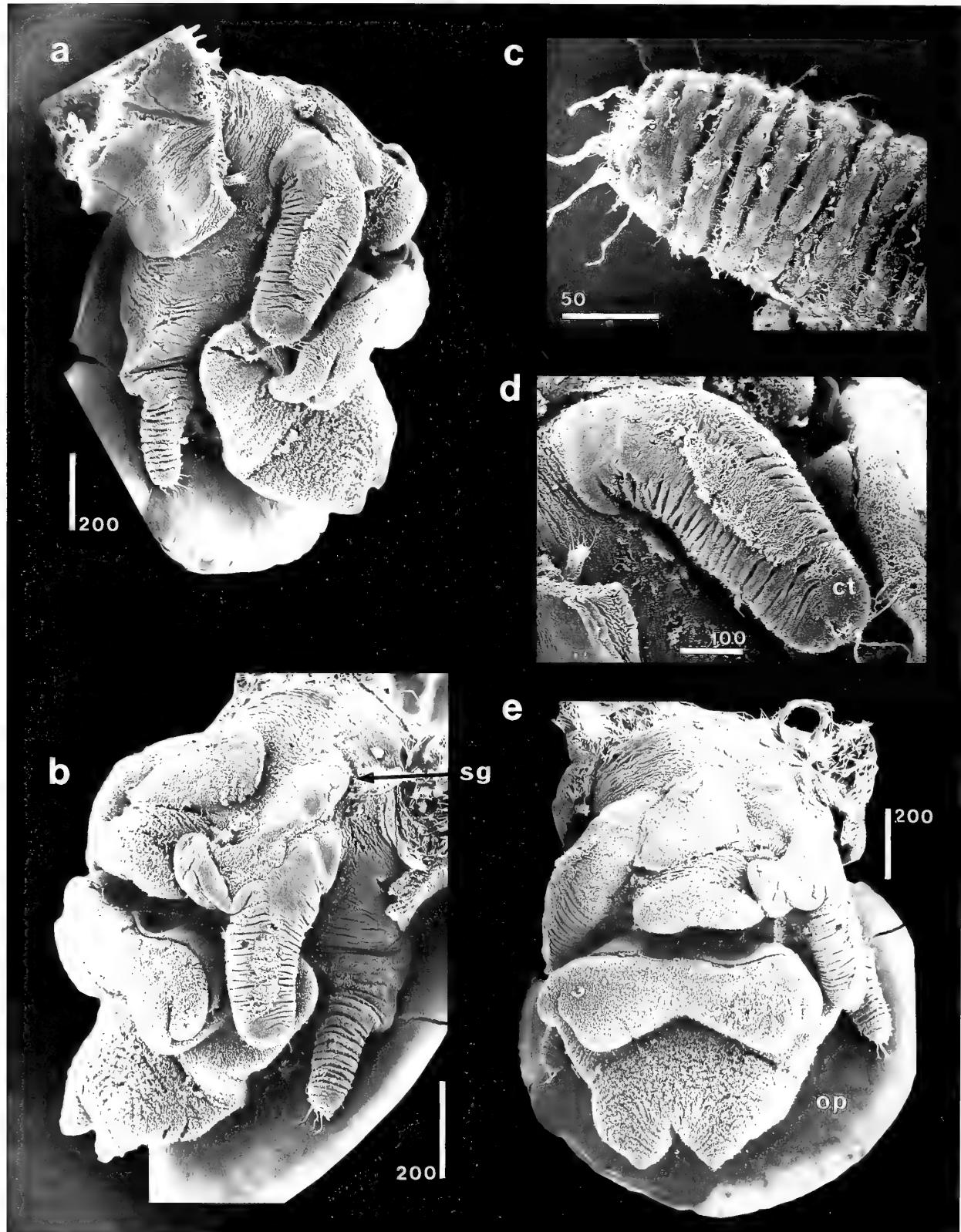
Distribution: JdF, Endeavour Segment, 2200 m depth.

Melanodrymia sp. “rust covered”

(Figures 21d, 24e, f)

Material examined: EPR at 13°N: - HERO 91 PL25 (Caldera), 10 spms; - HERO 91 PL27, 1 spm.

Description: The shape is roughly as in *M. aurantiaca*, but the shell lacks any trace of calcareous matter. Instead of a shell there is a solid cover of bacterially precipitated rust enveloping the periostracum, with a rich fauna of *Folliculina*-like ciliates (caeciform, 200–300 µm long and 70–80 µm in diameter, buried in the rust, only ap-



erture protruding). Radial ribs are visible on the periostracum around the umbilicus. The periostracum is thin and fragile and it is impossible to crack the rust without breaking the periostracum also. The maximum diameter is 3.2 mm.

Remarks: We do not know if the specimens described above represent a new species or specimens of *M. aurantiaca* which for some reason have not been able to form a shell. Such a phenomenon is known for *Depressiglyra globulus* which at one locality of the JdF was found and observed alive without a shell, the body surrounded only by the periostracum (Tunnicliffe & Fontaine, 1987).

The shape of the interior is closest to *M. aurantiaca*, but the specimens occurred sympatrically with this species so it is difficult to explain why some specimens form a shell and some do not. Furthermore, the shape and the structure of the rust cover is very uniform in all specimens, not variable in thickness and shape as in species of *Lirapex* and *Pachydermia* which often have deposits of comparable thickness. The external morphology of the soft parts and radula could, however, not be distinguished from *M. aurantiaca*.

One female, egg diameter in gonad ca. 130 µm, had two lanceolate objects, supposed to be spermatophores, attached in the rear part of the pallial cavity, with a kind of outer, transparent cover and inner fibrous structure, size 350 × 80 µm. Two more females lacked these. This is the first evidence of spermatophores in the Neomphalina.

Melanodrymyia galeronae Warén & Bouchet, sp. nov.

(Figures 15k, 16f, 21c, 24a, b, d)

Type material: Holotype, 5 dry and 11 alcohol paratypes in MNHN.

Type locality: EPR at 13°N, HERO 91 PL25, 10 km south of main locality, 12°42.65'N, 103°54.65'W, 2563 m, at the "Caldera."

Material examined: The types and: EPR at 13°N: - HERO 92 dive 2528, 1 specimen.

Distribution: EPR at 13°N, at about 2600 m depth.

Etymology: Named after Joëlle Galeron at IFREMER, who has sorted much of the material from the French deep-sea program.

Description: Shell (Figures 24a, b, d). Tall and sturdy, with thin, transparent periostracum, a strong peripheral

keel, oblique axial ribs, obliquely radiating axial striae, and shallow umbilical crevice in young specimens. The protoconch (Figure 15k) is completely covered by a fine net sculpture, consists of ¾ of a whorl, and has a distinctly expanded peristome. Its diameter is 250 µm. The teleoconch has up to 3.5 distinctly shouldered whorls. They have a very strong peripheral keel and a weaker basal one which connects to the basal corner of the peristome; up to 16 strong, oblique axial ribs which fade away at the keel and a second set of similar, obliquely aligned, basal ribs which reach this keel. In addition there is a much finer and uniform striation of irregular, sometimes double, obliquely radiating raised lines which are generated close to the suture by dichotomy of earlier lines. The columella is sturdy with the lower part of the inner lip reflected over it.

Dimensions. Maximum shell height 3 mm.

Operculum (Figure 16f) and **soft parts** as in *Melanodrymyia aurantiaca* (see Warén & Bouchet, 1989, Haszprunar, 1989a, Israelsson, 1998).

Radula (Figure 21c). Ca. 20 - 4 - 1 - 4 - 20. The marginal teeth are fewer in number than normal in Neomphalina. The central tooth is dominated by the anterior supporting ridges, and the apical plate is weakly serrated. The inner three laterals are much more slender than the fourth and they have a single denticle on the inner side of the main cusp; number four has a denticle on its outer side also. The marginals are flat; the inner ones with a handlike apical part with one major cusp, flanked by two to three smaller ones on each side; more laterally the cusps become smaller and the outermost teeth are finely serrated apically.

Remarks: This new species can easily be recognized by, contrary to previously described species of *Melanodrymyia*, being much taller than broad. We have examined the soft parts only very superficially, in order to save material if needed for future work, and also since from the shell morphology there seems little reason to question the systematic position.

Pachydermia Warén & Bouchet, 1989

Pachydermia Warén & Bouchet, 1989: 75.

Type species: *P. laevis* Warén & Bouchet, 1989; by original designation; hydrothermal vents at EPR.

Pachydermia laevis Warén & Bouchet, 1989

Pachydermia laevis Warén & Bouchet, 1989:76, figs. 28-29, 34, 37-40, 41, 42, 76, 85-86.

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Figure 25. *Retiskenea* cf. *diploura* Warén & Bouchet, gen. & sp. nov., Oregon Margin. a. Head-foot, right side. b. Head-foot, left side. c. Tip of epipodial tentacle. d. Right cephalic tentacle. e. Head-foot, front view. ct - cephalic tentacle; op - operculum; sg - sperm groove. Scale bars in µm.

Pachydermia laevis: Warén & Bouchet, 1993:40; Israelsson, 1998:95.

New records: EPR at 13°N: - HERO 91 PL05, 14 spms; - HERO 91 PL12, 25 spms; - HERO 91 PL17, 2 spms; - HERO 91 PL19, 42 spms; - HERO 91 PL21, 31 spms; - HERO 91 PL25 (Caldera), 5 spms; - HERO 91 PL26, 161 spms; - HERO 92 dive 2516, 2 spms; - HERO 92 dive 2517, 1 spm; - HERO 92 dive 2524, 2 spms; - HERO 92 dive 2526, 1 spm; - HERO 92 dive 2528, 1 spm; - HERO 92 dive 2531, 3 spms. EPR at 09°50'N: - HERO 91 PL09, 2 spms. EPR at 17°S: - NAUDUR PL06, site Rehu, 5 spms; on mussels, 1 spm.

Distribution: EPR from 21°N to 17°S, in 2500–2600 m depth.

Remarks: Almost all new specimens come from vestimentiferan tubes, but from earlier samplings, the species seems to be more common on other substrates.

Planorbidella Warén & Bouchet, 1993

Planorbidella Warén & Bouchet, 1993:35.

Type species: *Depressigyrta planispira* Warén & Bouchet 1989; by original designation; hydrothermal vents at EPR.

Planorbidella planispira (Warén & Bouchet, 1989)

Depressigyrta planispira Warén & Bouchet, 1989:81, figs. 48–50, 53, 54, 74, 84.

Planorbidella planispira: Warén & Bouchet, 1993:37, fig. 29D.

New records: EPR at 13°N: - HERO 91 PL10, 1 spm; - HERO 91 PL11 (Genesis), 8 spms; - HERO 91 PL17, 2 spms; - HERO 91 PL19, 3 spms; - HERO 91 PL21, 7 spms; - HERO 91 PL26, 3 spms; - HERO 92 dive 2523, 1 spm. EPR at 17°S: - NAUDUR PL06, site Rehu, 2 spms.

Distribution: EPR from 21°N to 17°S, in 2500–2600 m depth.

Neomphalus McLean, 1981

Neomphalus McLean, 1981:294.

Type species: *N. frettterae* McLean, 1981; by original designation; hydrothermal vents at the Galapagos Rift.

Neomphalus frettterae McLean, 1981

Neomphalus frettterae McLean, 1981:294, figs. 1–10.

Neomphalus frettterae: Warén & Bouchet, 1993:33.

New records: EPR at 13°N: - HERO 92 dive 2522, 2 spms (diameter 1.1 mm).

Distribution: EPR, 21°N to 09°50'N and the Galapagos Rift at about 2400–2600 m depth.

Remarks: The larva of *Neomphalus frettterae* was identified from plankton samples taken a few meters above the sea floor at the EPR at 09°50'N (Mullinéaux et al., 1996).

Lacunoides Warén & Bouchet, 1989

Lacunoides Warén & Bouchet, 1989:72.

Type species: *L. exquisitus* Warén & Bouchet, 1989; by original designation; Galapagos Rift vents.

Remarks: The new species described below is quite similar to the type species, although we have not been able to examine a male to verify that the left cephalic tentacle is modified to a copulatory organ. The operculum has the same kind of overlapping edges of the preceding whorls; the shell has very similar shape and sculpture (although the spiral sculpture is less conspicuous in *L. vitreus*), and the central tooth of the radula shares the same type of unusually large, flat, and elongate apical plate.

Lacunoides vitreus Warén & Bouchet, sp. nov.

(Figures 29a–e)

Type material: Holotype (FMNH 280088) and paratypes 2 spms dried, 1 empty sh (FMNH 280924), 6 spms wet (FMNH 280901) in FMNH; 2 paratypes in MNHN.

Type locality: JdE, Axial Seamount, Ashes vent field, 45°56.00'N, 130°00.86'W, 1543 m depth, ROPOS R406, in a “worm grab.”

Material examined: Only known from the type material.

Distribution: Only known from the type locality.

Etymology: “*vitreus*,” Latin, like glass, referring to the transparent, colorless shell.

Description: Shell (Figures 29c, d). Small, globular, transparent, with depressed spire, large aperture, and rapidly increasing diameter of whorls. The protoconch (Figure 29e), diameter 180 µm, consists of about half a whorl, is loosely coiled and initially covered by an irregular net-sculpture which becomes less obvious toward the distinctly expanded peristome. The teleoconch consists of about two whorls of rapidly enlarging diameter and round cross section. The first whorl is sculptured by weak incremental lines, which gradually become larger and after 1.1–1.2 teleoconch whorls form sharp axial low lamellae. One-tenth of a whorl later, also a much finer, dense spiral striation commences, which covers all the surface of the final half whorl. The peristome is round, not indented by the preceding whorl, thin and sharp, tangential and strongly prosocline.

Dimensions. Diameter of holotype, 2.4 mm; maximum diameter 2.5 mm.

Soft parts. The foot can be folded 180° to close the

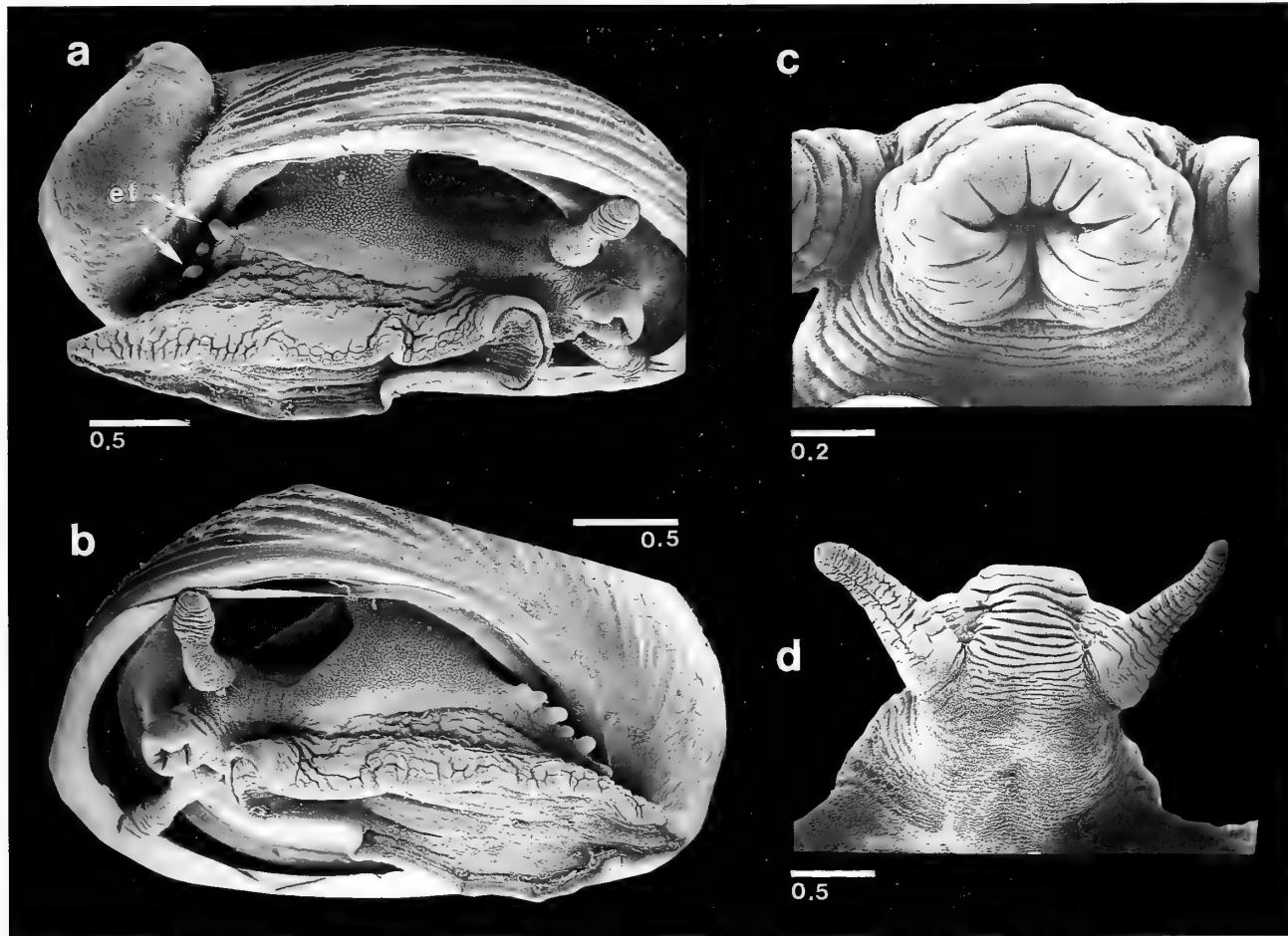


Figure 26. *Peltospira smaragdina* Warén & Bouchet, sp. nov., critical-point dried. *a*. Right side of animal. *b*. Left side of animal. *c*. Snout, ventral view. *d*. Dorsal view of head. *et* - epipodial tentacle. Scale bars in mm.

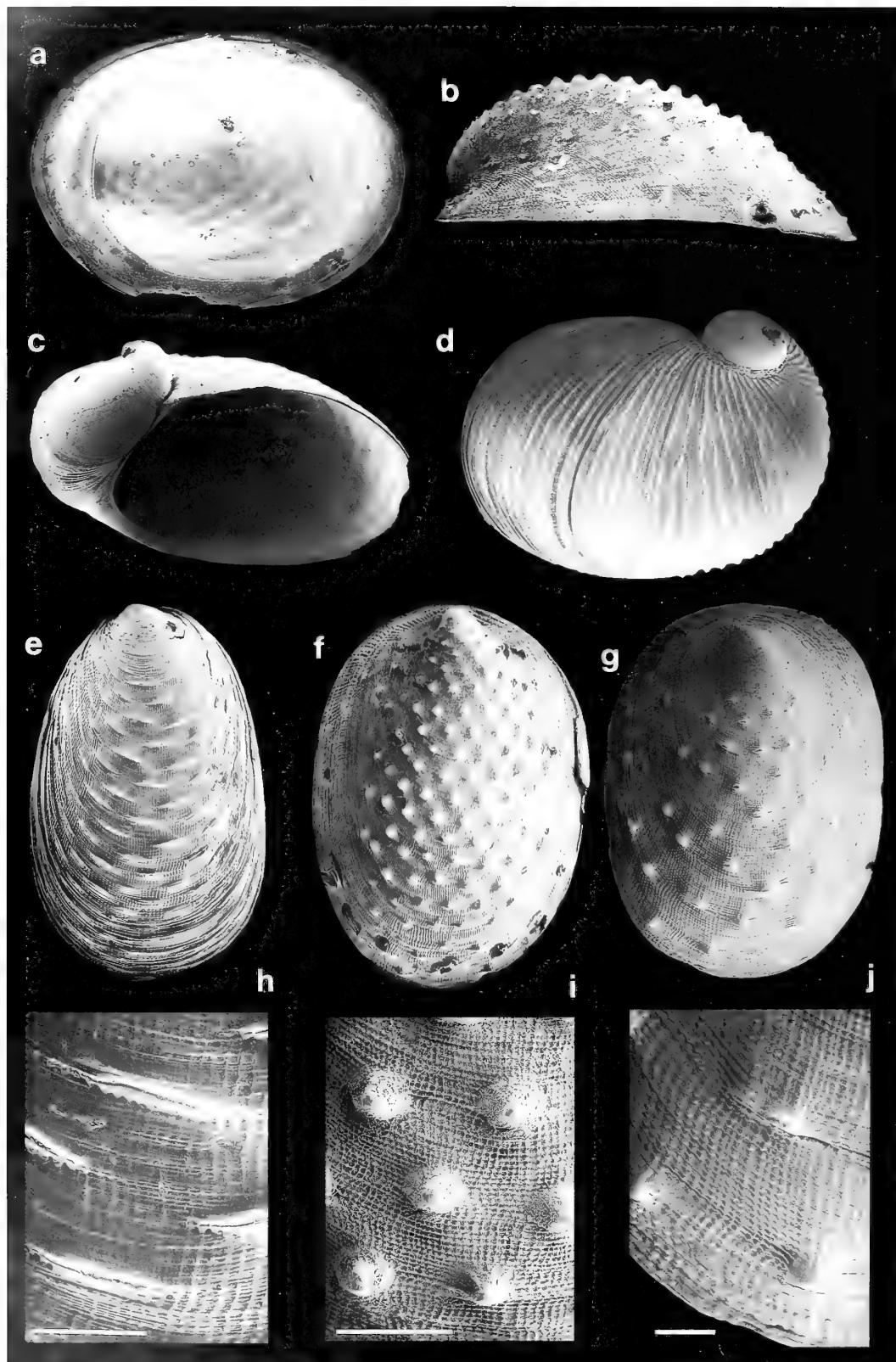
aperture (Figure 29c). The head is small, the cephalic tentacles slightly longer than the snout. The snout is apically strongly bilobed and drawn out to fine points. The presence of a ventral-lateral furrow could not be verified. Dorsally, across the neck, shortly behind the cephalic tentacles runs a well demarcated furrow. It starts behind the left cephalic tentacle, continues past the right one, turns to the right and backward at the right columellar muscle and fades out in the external pallial furrow. The end of its right side is flanked by a low skin-fold. The foot is large, low, and flat, anteriorly truncate and drawn out to small corner tentacles; posteriorly it is broadly rounded. A propodium is present. Posteriorly, along the sides, is a membrane with a series of five to six small epipodial tentacles under the operculum. No other appendices. The columellar muscle is very short, a narrow strip across the inner side of the aperture, distinctly enlarged at the right side. Its left side is mainly ventral and ends as a narrow wedge. The pallial margin is smooth. The gill is bipinnate with about 25 pairs of leaflets; it is restricted to the

left posterior quadrant of the pallial cavity, with a roughly diagonal direction. It is attached mainly by the efferent membrane which is unusually large. A transverse pallial vein runs from the posterior, right part of the gill to the anterior part of the rectum (joining the rectal sinus?).

Operculum (Figure 29c). Multispiral center bulging out in retracted specimens, thin and colorless, slightly larger than the aperture. The edge of previous whorl forms a distinct overlap over next whorl.

Radula (Figures 29a–b). Ca. 10-4-1-4-ca. 10. The central tooth has a long and slender, finely serrated, apical cutting plate, almost twice as long as that of the first lateral tooth. The lateral teeth have longer and more slender apical plate toward the side, with a serration similar to the central. The marginal teeth are oar-shaped with the apical third of the outer margin finely serrated. The serration is basally demarcated by a small spur. Toward the edge the marginals are more slender and lack the spur.

Remarks: This new species is an interesting addition to



the fauna of the JdF system, because it contributes to a reduction of the differences in generic composition between the vent systems. There should be no difficulties in recognizing this species. *Lacunoides exquisitus* from the Galapagos Rift, differs by having a much stronger spiral sculpture and a more widely spaced net sculpture on the protoconch.

Family PELTOSPIRIDAE McLean, 1989

Remarks: We have kept *Depressigryra* and *Lirapex* with the peltospirid limpets, since both have a protoconch similar to *Peltospira*.

Peltospira McLean, 1989

Peltospira McLean, 1989b:51.

Type species: *P. operculata* McLean, 1989; by original designation; EPR at 21°N.

Remarks: The species of *Peltospira* form a series in the degree of limpetization, from *P. lamellifera*, where the operculum is retained and of a size corresponding to the aperture. This species can also fold the foot 180° to close the aperture with the operculum. In *P. operculata* the foot can be folded only 90° and the species cannot close the aperture, although the operculum is large enough. In *P. delicata* and *P. smaragdina* the foot does not have a long, posterior "tail" for carrying the operculum, and the operculum is lost. They have thus achieved the limpet organization, although the foot is not as muscular and large as in patellogastropod or fissurellid limpets. It seems likely that the other limpetlike peltospirid genera simply are more advanced on this evolutionary pathway and that these genera may be paraphyletic. This, however, remains to be shown.

Peltospira smaragdina, Warén & Bouchet, sp. nov.

(Figures 15n, 26a–d, 27c, d, 31e, f)

Type material: Holotype and 43 paratypes in MNHN.

Type locality: MAR, Lucky Strike, ALVIN dive 2606, 37°17.55'N, 32°16.47'W, 1628 m, Statue de la Liberté.

Material examined: The types and: MAR, Menez Gwen: - DIVA 1 PL 14, on sulfide rock with Hydrozoa, 1 spm; - DIVA 2 PL 11, suction sample among mussels, 1 spm;

- DIVA 2 PL 12, 1 spm. *Lucky Strike*: - DIVA 1 PL 04, on inactive chimney among Hydrozoa and sponge *Cladorhiza*, 5 spms; - DIVA 1 PL 17, 42 spms; on a black smoker, 5 spms; - DIVA 2 PL 02, 231 spms, on sulfide flanges, 17 spms; - DIVA 2 PL 04, 1 spm; - DIVA 2 PL 05, 20 spms; - DIVA 2 PL 06, 1 spm; - DIVA 2 PL 07, 10 spms; - DIVA 2 PL 08, 1 spm; - DIVA 2 PL 09, suction sample among mussels and hydrothermal sediments, 1 sh; - DIVA 2 PL 10, 2 suction samples among mussels and hydrothermal sediments, 1 and 9 spms; - DIVA 2 PL 23, 2 spms; - DIVA 2 PL 25, 152 spms; - DIVA 2 PL 26, 1 spm; Sintra, 20 spms; - ALVIN dive 2606, 55 spms; - ALVIN dive 2607, 12 spms; - MARVEL PL1200, Bairro Alto, 0.25 m² rock surface close to edifice, 16 spms; - MARVEL PL1205, Bairro Alto, retrieval box, 2 spms. *Snake Pit*: - ALVIN dive 2613, from gut of a shrimp, 1 spm; - ALVIN dive 2618, 30 spms; - ALVIN dive 2620 on a smoker, 11 spms; - ALVIN dive 2622, 22 spms; - GRAVINAUT PL16, 53 spms. *Logatchev site*: - MICROSMOKE PL12 (Ruches), 3 spms; - MICROSMOKE PL20 (Irina), 15 spms.

Distribution: MAR, from Menez Gwen to Logatchev site, in 850–3500 m, mainly on rocks in the vicinity of vents.

Etymology: "smaragdina" from the bright green color of the periostracum of perfect specimens.

Description: *Shell* (Figures 27c, d). Of medium size for its group, haliotiform, with very rapidly increasing diameter, fragile, with thick greenish periostracum, usually axially ridged. The protoconch (Figure 15n) has no obvious coiling and is sculptured by about 12 "spiral" ridges which do not reach the slightly expanded peristome. The diameter is 250 µm. The teleoconch consists of about 1.7 whorls of rapidly increasing diameter, and is sculptured by regularly spaced, strong axial ribs, which give the shell an appearance of corrugated sheet metal. The spiral striation varies in distinctness and strength. The outer lip is not thickened, the inner lip forms a thickened callus on the columella. The periostracum is tough, thick, dark greenish, reflected across the shell margin.

Dimensions. Maximum diameter of shell 12 mm.

Soft parts (Figures 26a–d). The foot is muscular and fleshy, anteriorly broadly rounded, posteriorly tapering; the propodium demarcated by a narrow fissure. The sides of the foot are covered by irregularly shaped tubercles. The epipodium consists of about 10 irregularly shaped

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Figure 27. Peltospiridae, shells. a, b, f, i. *Nodopelta rigneae* Warén & Bouchet, sp. nov., holotype, diameter 7.1 mm. a. Ventral view. b. Lateral view, right side. f. Apical view. i. Detail of sculpture. c, d. *Peltospira smaragdina* Warén & Bouchet, sp. nov., Menez Gwen. c. Apertural view, diameter 3.6 mm. d. Dorsal view, diameter 9.4 mm. e, h. *Nodopelta subnoda*, EPR, 13°N. e. Dorsal view, 8.4 mm. h. Detail of sculpture. g, j. *Nodopelta heminoda*, EPR, 13°N. g. Dorsal view, 11.0 mm. j. Detail of sculpture, notice that the magnification is only half of Figures h and i. Scale bars 0.5 mm.

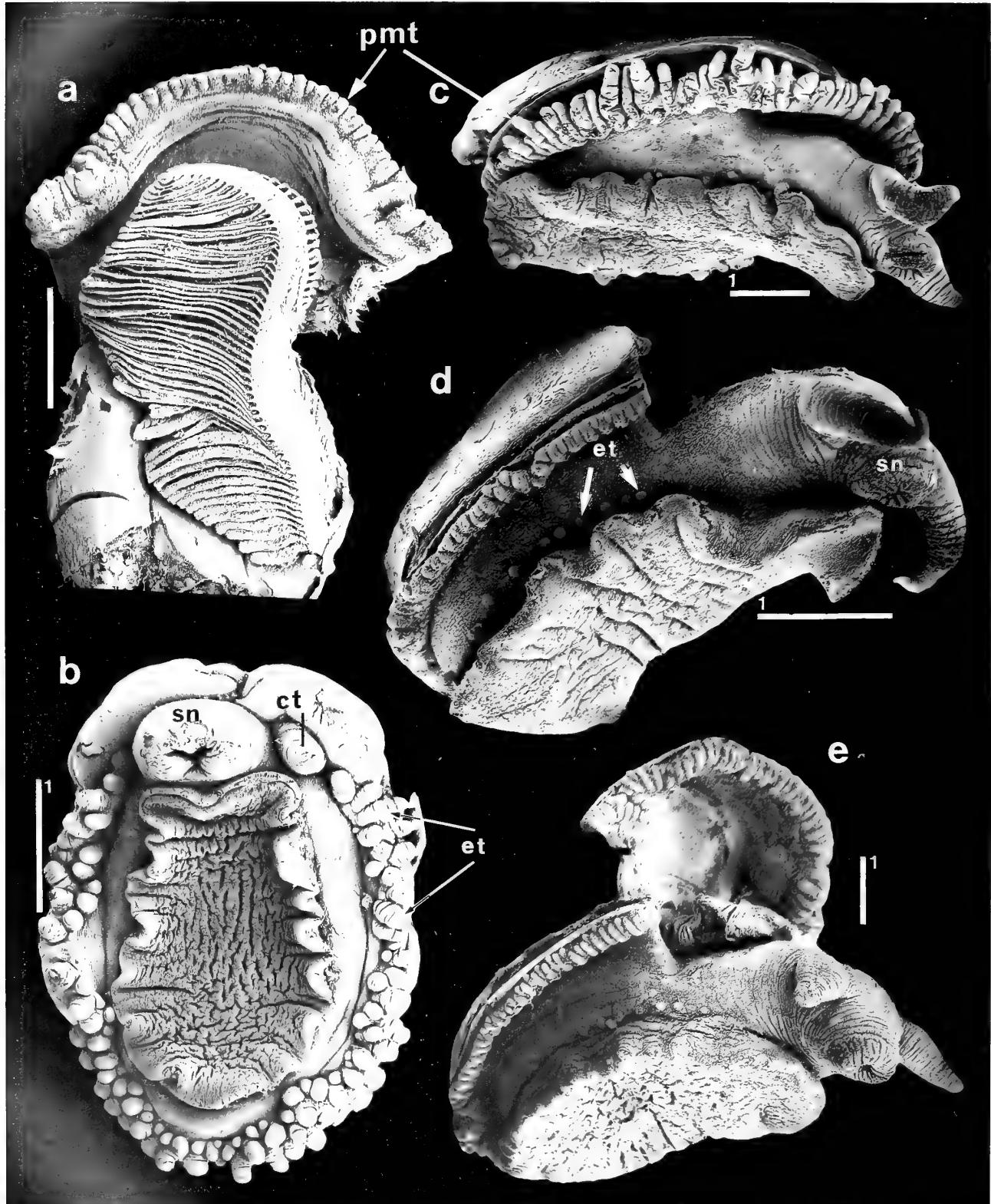


Figure 28. Peltospirid limpets, critical-point dried. *a, d. Nodopelta rigneae* Warén & Bouchet, sp. nov., holotype. *a*. Pallial skirt. *d*. Head-foot, right side, left side of foot removed. *b*. *Echinopelta fistulosa*. EPR at 13°N. *c*. *N. subnoda*, EPR at 13°N. *e*. *N. heminoda*, EPR at 13°N. ct - cephalic tentacle; et - epipodial tentacle; pmt - pallial margin tentacle; sn - snout. Scale bars in mm.

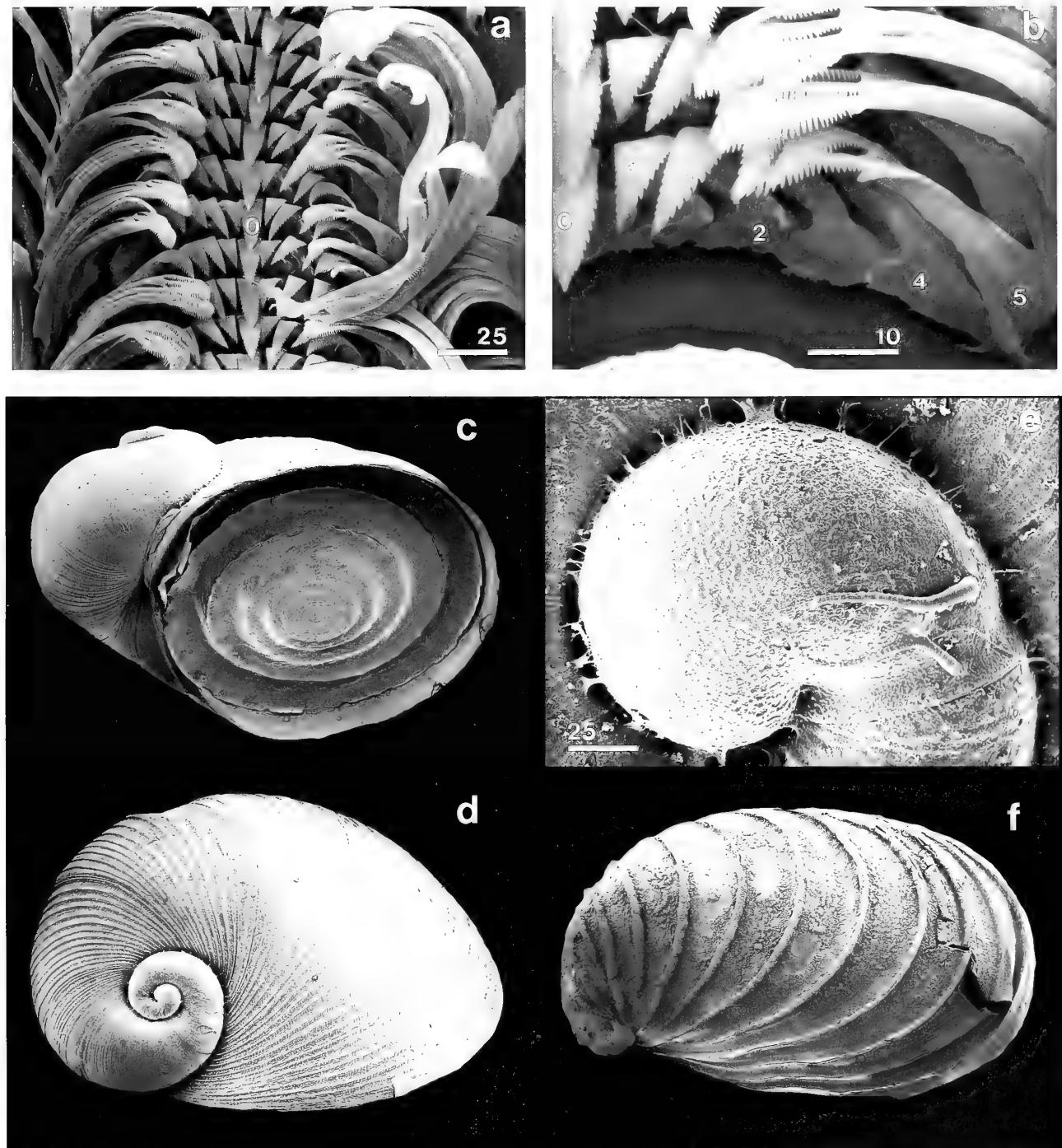


Figure 29. a–e. *Lacunoides vitreus* Warén & Bouchet, sp. nov. Teeth numbered sequentially with central tooth as 0. a, b. Radula, outermost lateral tooth is number 4. c–e. Shells. c. Holotype, diameter 2.4 mm. d, e. Paratype, diameter 2.2 mm. f. *Peltospira delicata*, unusually strongly sculptured specimen, maximum diameter 4.5 mm. EPR at 13°N. Scale bars in μm .

tentacles and papillae on a low ridge along the posterior $\frac{1}{5}$ of the foot; more anteriorly the ridge levels out and disappears on the neck. Just above the two most posterior epipodial tentacles is a small pore, perhaps some rudiment of the operculum. The head is well demarcated, rather slender with tapering snout and a pair of long, tapering cephalic tentacles, more than twice the length of the snout and without a trace of eyes. The snout has an apical demarcating ridge and an almost ventral mouth. There are no cephalic lappets or other cephalic appendages. The pallial margin is tripartite with periostracum adhering in the inner furrow. The gill is very large, bipectinate, both axes attached for half their length. There are no sensory bursicles visible in the adult, and cephalic and epipodial tentacles lack sensory papillae. The shell muscle is almost aequilateral; the left part slightly more slender and narrow. There are no external differences between the sexes and no ciliated sperm tract was found in the males.

Operculum. Lost at a size below 1 mm.

Radula (Figures 31e-f). n - 4 - 1 - 4 - n. The whole central field is quite narrow and its teeth considerably lower than the marginals. Its teeth are sturdy and interlocking, but only the outermost one has denticles, and only along the outer side of the apical plate. The inner marginals are the shortest; they are flat, aligned in the direction of the row, and have an apical, truncate, reflected serration. Farther laterally the teeth are densely packed with the flat side at right angle to the earlier ones and a deeply serrated scyphelike apical part above a basal spur. *Jaw.* Thin and membranous, no prisms visible.

Remarks: The sculpture of *P. smaragdina* is variable, and the spiral striation is often absent; the axial ribbing may also be absent especially on the early spire. The gut contains sediment and mineral particles.

Peltospira delicata McLean, 1989

(Figure 29f)

Peltospira delicata McLean, 1989b:53, figs. 9-16.

New records: EPR at 13°N: - HERO 91 PL21, 1 spm; - HERO 92 dive 2519, 1 spm; - HERO 92 dive 2520, 1 spm; - HERO 92 dive 2521, 2 spms; - HERO 92 dive 2522, 1 spm; - HERO 92 dive 2531, 1 spm. EPR at 09°50'N: - HERO 91 PL09, 2 spms. EPR at 17°S: - NAUDUR PL08, 1 spm; - NAUDUR PL09 (Fromveur), 1 spm; - NAUDUR PL18.4.8b, site Rehu, 12 spms.

Distribution: EPR from 13°N to 17°S, at 2500-2600 m depth.

Remarks: Almost all specimens come from vestimentiferan tubes. The sculpture of the shell is quite variable; some specimens have strong axial ribs (Figure 29f), others are smooth; most are intermediate.

Peltospira operculata McLean, 1989

Peltospira operculata McLean, 1989b:51, figs. 1-8.

New records: EPR at 13°N: - HERO 91 PL04, 20 spms, 12 young; - HERO 91 PL11, 11 spms; Genesis, 8 spms; - HERO 91 PL13, 15 spms; - HERO 91 PL14 (Elsa), 4 spms; - HERO 91 PL18, 83 spms; - HERO 91 PL20, 8 spms; - HERO 91 PL21, 1 spm; - HERO 91 PL24 (Elsa), 1 spm; - HERO 91 PL26, 1 spm; - HERO 91 PL27 (Totem), 2 spms; - HERO 92 dive 2516, 13 spms; - HERO 92 dive 2519, 8 spms; - HERO 92 dive 2520, 20 spms; - HERO 92 dive 2521, 1 spm; - HERO 92 dive 2523, 3 spms; - HERO 92 dive 2524, 2 spms; - HERO 92 dive 2525, 2 spms; - HERO 92 dive 2532, 4 spms. EPR at 09°50'N: - HERO 91 PL06, 2 spms. EPR at 17°S: - NAUDUR PL18.4.8b, site Rehu, 1 spm.

Distribution: EPR from 21°N to 17°S, at a depth of 2500-2600 m.

Remarks: Most specimens above were obtained from tubes of vestimentifera, but the species probably has its main distribution on rocks, since it is proportionally more common in such samples.

The larva of *P. operculata* was identified in plankton samples taken a few meters above the sea floor at the EPR at 09°50'N (Mullineaux et al., 1996).

Peltospira lamellifera Warén & Bouchet, 1989

(Figures 16k, 46b, 48c, d)

Peltospira lamellifera Warén & Bouchet, 1989:74, fig. 24.

New records: EPR at 13°N: - HERO 91 PL05, 1 spm; - HERO 92 dive 2516, 1 spm.

Distribution: Only known from the EPR at 13°N, ca. 2600 m depth.

Remarks: These are only the second and third specimens known of this species. The soft parts can be retracted into the shell and the aperture entirely closed by the operculum at a size of 1.2 mm shell diameter. The holotype is larger than the two new specimens, 2.1 mm, but was an empty shell, and the ability to completely retract the soft parts was not known.

We figure a critical-point dried specimen (Figure 46b); although poorly preserved and contracted, it shows clearly the basic difference from the species of the limpet stage, i.e., the foot folded 180° and the aperture completely closed by the operculum. The protoconch is not known, but the simple snout and radular morphology (Figures 48c, d) indicate that this species really is a peltospirid.

Nodopelta McLean, 1989

Nodopelta McLean, 1989b:53.

Type species: *N. heminoda* McLean, 1989; by original designation; hydrothermal vents at EPR.

Nodopelta heminoda McLean, 1989
 (Figures 27g, j, 28e)

Nodopelta heminoda McLean, 1989b:53, figs. 17–23.

New records: EPR at 13°N: - HERO 91 PL12, 1 spm; - HERO 91 PL18, 2 spms; - HERO 91 PL26, 1 spm; - HERO 92 dive 2517, 1 spm.

Distribution: EPR at 21°N and 13°N, at about 2600 m depth.

Remarks: We figure *N. heminoda* for comparison with *N. subnoda* and *N. rigneae*, from which it differs by its larger size, and more widely scattered tubercles.

Nodopelta subnoda McLean, 1989
 (Figures 27e, h; 28c)

Nodopelta subnoda McLean, 1989b: 56, figs. 24–31.

New records: EPR at 13°N: - HERO 91 PL04, 30 spms; - HERO 91 PL05, 5 spms. EPR at 17°S: - NAUDUR PL06, site Rehu, 3 spms; - NAUDUR PL18 (Le Chat), 1 spm; - NAUDUR PL18.4.8b, site Rehu, 9 spms.

Distribution: EPR from 21°N to 17°S, at a depth of 2500–2600 m.

Remarks: Six specimens from HERO 91 PL04, smaller than 4–5 mm, have shorter tubercles on the inner part of the pallial fold, and the pallial margin tubercles are thus arranged in a more or less double row. Regrettably all these specimens had lost their shell before we received them and we can not say if this is a juvenile character or if one more species is involved. We figure *N. subnoda* for comparison with *N. heminoda* and *N. rigneae*.

Nodopelta rigneae Warén & Bouchet, sp. nov.
 (Figures 21e, f, 27a, b, f, i, 28a, d)

Type material: Holotype and two paratypes in MNHN.

Type locality: EPR at 13°N, site Elsa, 12°48.09'N, 103°46.34'W, 2630 m depth, from vestimentiferan washings.

Material examined: EPR at 13°N: - HERO 92 dive 2517, 2 spms, paratypes.

Distribution: Only known from the type locality.

Etymology: Named after Mrs. Kerstin Rigneus (SMNH) who sorted and identified much of the material used for this paper.

Description: Shell (Figures 27a, b, f, i). Haliotiform, of medium size for the group, ovate, convex, pustulose with thick, brown periostracum. The protoconch is not known. The shell is 2.9 times as long as high and the apex is situated 2–4% of the length in front of the posterior mar-

gin. The whole shell is covered by a fine sculpture (Figure 27i) of concentric ridges and tubercles, the latter giving an impression of a radial striation. There are also strong tubercles, diameter 0.15–0.20 mm, more concentrated over the central part of the shell. The periostracum is reflected across the margin of the shell. The posterior inside is strengthened by a strong, convex shelf of a maximum width corresponding to about $\frac{1}{10}$ of the diameter of the shell. The muscle scar is indistinct, horseshoe-shaped with the anteriorly wider and rounded limbs reaching the anterior $\frac{1}{3}$ of the shell. The peristome is almost perfectly flat.

Dimensions. Diameter of the holotype 7.1 mm, maximum diameter 8.7 mm.

Soft parts (Figures 28a, d). Normal for the genus; pallial margin with a single series of small, short tentacles of even size all along its circumference. The epipodial tentacles are small and inconspicuous, about 15 in number along each side and cover almost the whole length of the foot.

Radula (Figures 21e–f). As for genus, slender, n – 4 – 1 – 4 – n, end of radular sac bilobed. The outermost lateral tooth is weakly serrated along the outer side of the apical plate. The change to the marginals is abrupt. The marginal teeth are flat, apically truncated at right angle, have a series of recurved comblike denticles and, below these, a small spur at each side.

Remarks: *Nodopelta rigneae* differs from *N. heminoda* by being smaller, having a finer sculpture, and the tubercles are more concentrated to the central part of the shell. During dive 2517 it was collected with *N. heminoda*. *Nodopelta subnoda* is much flatter, has elongate sculptural elements, and the apex is situated outside (behind) the peristome.

Hirtopelta McLean, 1989

Hirtopelta McLean, 1989b:60.

Type species: *H. hirta* McLean, 1989; by original designation; hydrothermal vents at EPR.

Hirtopelta hirta McLean, 1989

Hirtopelta hirta McLean, 1989b:62, figs. 49–55.

Hirtopelta hirta: Warén & Bouchet, 1993:35, fig. 26a–c.

New records: EPR at 13°N: - HERO 92 dive 2523, 1 spm.

Distribution: EPR from 21°N to 13°N, at a depth of 2500–2600 m.

Remarks: This and the following species are known from very few specimens, and only from 13°N at the EPR.

Ctenopelta Warén & Bouchet, 1993*Ctenopelta* Warén & Bouchet, 1993:33**Type species:** *C. porifera* Warén & Bouchet, 1993; by original designation; hydrothermal vents at EPR.*Ctenopelta porifera* Warén & Bouchet, 1993*Ctenopelta porifera* Warén & Bouchet, 1993:34, figs. 26D–G, 27A–F, 28A–D.**New records:** EPR at 13°N: - HERO 92 dive 2512, 1 spm; - HERO 92 dive 2528, 1 spm.**Distribution:** EPR at 13°N, ca. 2600 m depth.**Remarks:** *Ctenopelta porifera* is usually badly discolored by sulfides, and the pores penetrating the shell may perhaps be involved in chemosynthetic activity.*Echinopelta* McLean, 1989*Echinopelta* McLean, 1989b:58.**Type species:** *E. fistulosa* McLean, 1989; by original designation; hydrothermal vents at EPR.*Echinopelta fistulosa* McLean, 1989

(Figure 28b)

Echinopelta fistulosa McLean, 1989b:60, figs. 41–48.**New records:** EPR at 13°N: - HERO 91 PL04, 9 spms; - HERO 91 PL05, 1 spm.**Distribution:** EPR at 21°N and 13°N, at a depth of about 2600 m.**Remarks:** This is the first record outside the type locality. The specimens were found in residues from tubes of vestimentifera. We figure a critical-point dried specimen for comparison with the species of *Nodopelta*, to show the abundance of epipodial tentacles.*Rhynchopelta* McLean, 1989*Rhynchopelta* McLean, 1989b:57.**Type species:** *R. concentrica* McLean, 1989; by original designation; hydrothermal vents at EPR.*Rhynchopelta concentrica* McLean, 1989*Rhynchopelta concentrica* McLean, 1989b:58, figs. 32–40.**New records:** EPR at 13°N: - HERO 91 PL 13, 14 spms; - HERO 91 PL 11 (Genesis), 8 spms; - HERO 91 PL 17, 13 spms; - HERO 91 PL 19, 34 spms; - HERO 91 PL 21, 74 spms; - HERO 91 PL 26, 57 spms; - HERO 92 dive 2512, 8 spms; - HERO 92 dive 2514, 1 spm; - HERO 92 dive 2516, 3 spms; - HERO 92 dive 2517, 77 spms; - HERO 92 dive 2519, 1 spm; - HERO 92 dive

2521, 1 spm; - HERO 92 dive 2523, 1 spm; - HERO 92 dive 2524, 8 spms; - HERO 92 dive 2528, 1 spm; - HERO 92 dive 2531, 3 spms. EPR at 09°50'N: - HERO 91 PL 09, 1 sh. EPR at 17°S: - GEOCYARISE 84, 17°26'S, 113°12'W, 2600 m, 1 spm.

Distribution: EPR from 21°N to 17°S, ca. 2500–2600 m, usually living on tubes of Vestimentifera.**Remarks:** The larva of *R. concentrica* was identified in plankton samples taken a few meters above the sea floor at the EPR at 09°50'N (Mullineaux et al., 1996).*Lirapex* Warén & Bouchet, 1989*Lirapex* Warén & Bouchet, 1989:84.**Type species:** *L. humata* Warén & Bouchet, 1989; by original designation; vents at the EPR at 21°N.**Remarks:** The three species now classified in *Lirapex* share the presence of axial sculpture, usually most developed at the shoulder of the whorls and hooklike marginal teeth (flat, truncated with recurved comblike apical serration in *Depressigryra*).*Lirapex costellata* Warén & Bouchet, sp. nov.

(Figures 15m, 16i, 30a–c, 31a–c)

Type material: Holotype and 7 paratypes in MNHN.**Type locality:** MAR, Lucky Strike, DIVA 1 PL 04, Tour Eiffel, 37°17.32'N, 32°16.51'W, 1685 m, on inactive chimney among Hydrozoa and the sponge *Cladorhiza*.**Material examined:** Lucky Strike: - DIVA 1 PL 04, in baited trap, 3 spms; - DIVA 2 PL 04, 12 spms; suction sample among mussels in shimmering water, 1 spm; - DIVA 2 PL 07, 2 suction samples among mussels and hydrothermal sediments, 6 and 2 spms; - DIVA 2 PL 10, suction sample among mussels and hydrothermal sediments, 1 spm, retrieval box, 1 spm; - DIVA 2 PL 24, 3 spms; - DIVA 2 PL 25, 2 spms; - MARVEL PL1191, Bairro Alto, suction sample, 1 spm; - MARVEL PL1195, Tour Eiffel, 1685 m, retrieval box, 5 spms.**Distribution:** Only known from the MAR at the Lucky Strike site, 1600–1700 m, among mussels and in sediment.**Etymology:** “*costellata*,” Latin, with small ribs.**Description:** Shell (Figures 30a–c). Of medium size for the group, skeneimorph, rather sturdy, brownish, with axial ribs, usually covered by thick crusts of rust, with umbilicus and partly detached last whorl. Protoconch (Figure 15m) with indistinct coiling, with about half a dozen, strong, spirally directed ridges on its initial part, later smooth, and with slightly expanded peristome. Diameter 250 µm. The teleoconch has 2.5–3 whorls of almost

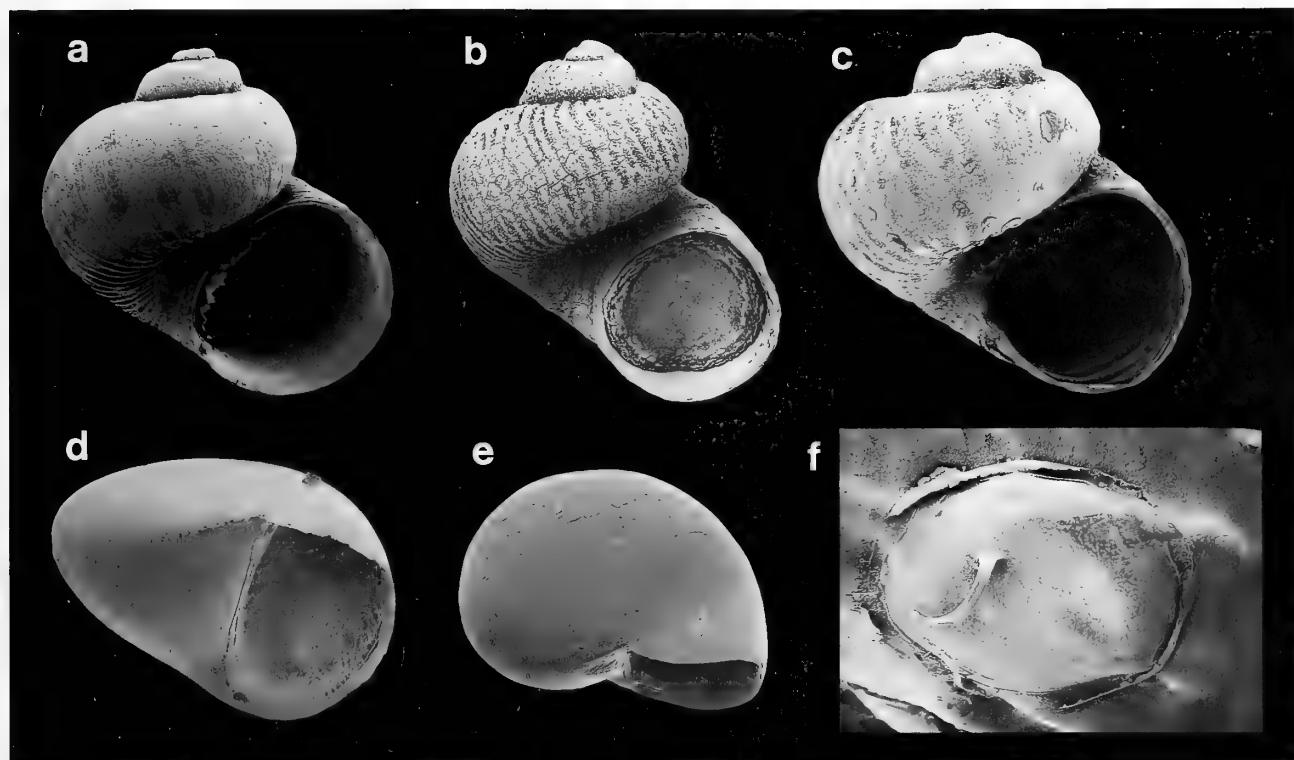


Figure 30. a–c. *Lirapex costellata* Warén & Bouchet, sp. nov., paratypes, Lucky Strike. a. Diameter 2.7 mm. b. Diameter 3.2 mm. c. Young, diameter 2.1 mm. d–f. *Bathynerita naticoidea*, Bush Hill Seep. d, e. Larval shells from egg capsules (protoconch 1), diameter 135 µm and 150 µm. f. Egg capsule, diameter 1.3 mm.

round cross section and axial, prosocline, thick and rounded ribs. The ribs are highly variable in their development, sometimes crowded and strong, sometimes more distant, sometimes only traces remain at the shoulder and base of the body whorl. The outer lip is simple and slightly thickened. The umbilicus is not very broad and in adult specimens obscured by the detachment of the last $\frac{1}{4}$ whorl.

Dimensions. Maximum shell height 3.2 mm at a diameter of 3.6 mm.

Soft parts. The foot is flat and muscular, anteriorly bluntly rounded with well developed propodium and the corners drawn out to small tentacles. The epipodial arrangement could not be worked out in detail, but there are at least five tentacles at each side, placed rather far back. The head is large with a short snout and subventral mouth. The cephalic tentacles are short, conical, and stout (contracted). No sensory papillae, neck-lobes or cephalic lappets. The pallial margin lacks appendages. The gill is bipectinate and seems to lack bursicles.

Operculum (Figure 16i). Brown, multispiral with about 12 whorls, concentric nucleus, and short growth zone.

Radula (Figures 31a–c). n-4-1-4-n. The central tooth has a triangular, smooth apical plate. The three inner lateral teeth are uniform, with smooth apical plates, the

fourth one is more obliquely directed, broader, and has a small serration at each side of the large main cusp. The marginal teeth are densely packed, the innermost two to three equipped with a triangular cusp and a few denticles, the outer ones have a series of five to seven apical, longitudinally arranged hooks.

Remarks: The four specimens (from different samples) used for examination of the soft parts were all rather poorly preserved and little information could be extracted. The position in *Lirapex* seems, however, quite certain, judging from good similarity in shell and radula and no remarkable deviations in the soft parts.

Lirapex sp. nov.

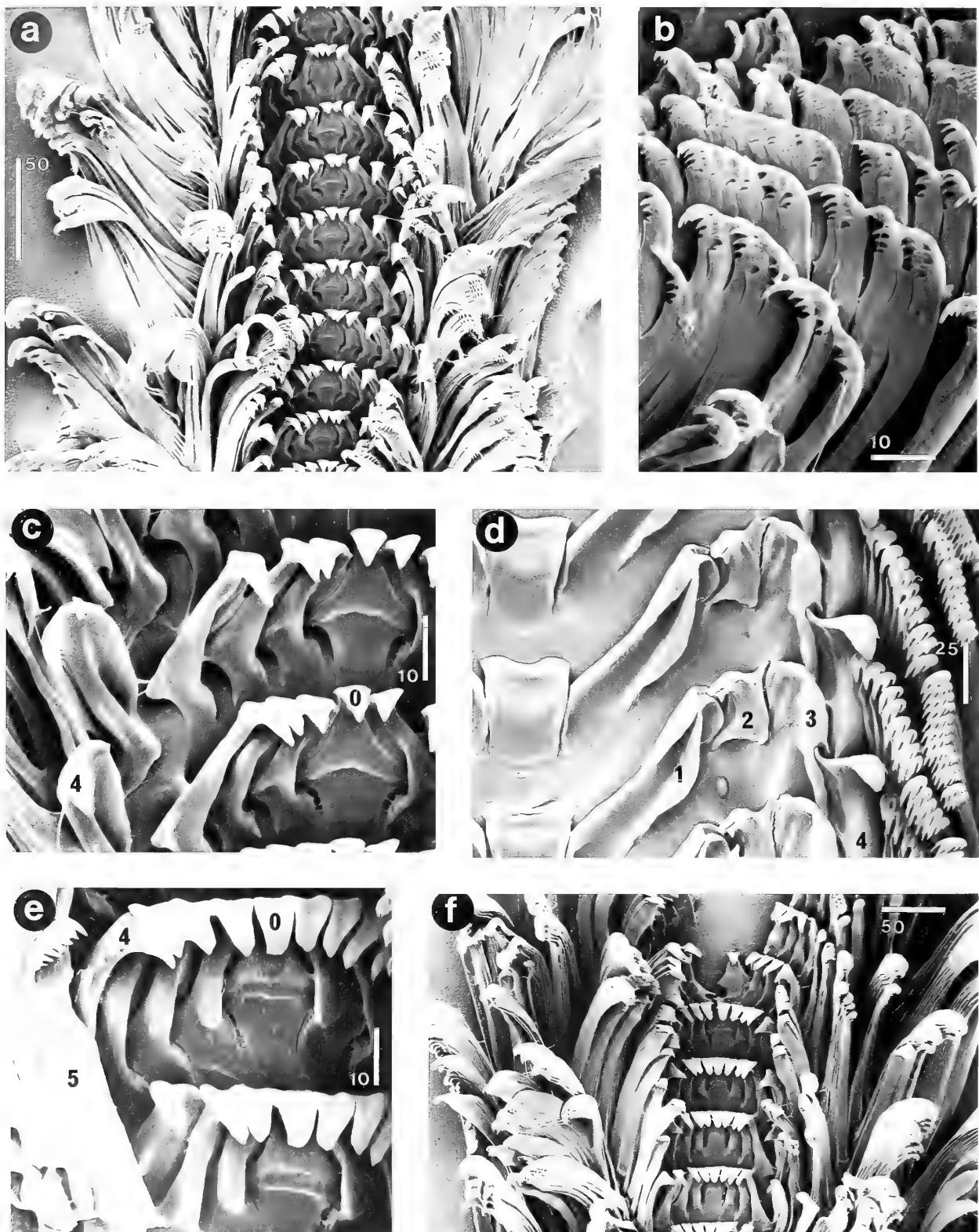
Material examined: MAR at Snake Pit: - ALVIN dive 2615, 3 shs.

Remarks: Three shells were found, but none had a protoconch left and the systematic placement is based mainly on intuition.

Depressigyra Warén & Bouchet, 1989

Depressigyra Warén & Bouchet, 1989:80.

Type species: *D. globulus* Warén & Bouchet, 1989; by original designation; hydrothermal vents at EPR.



Depressigyra globulus Warén & Bouchet, 1989

(Figure 15o)

Depressigyra globulus Warén & Bouchet, 1989:80, figs. 30–31, 45–47, 51–52, 73, 83.*Depressigyra globulus*: Warén & Bouchet, 1993:35.

New records: JdF, Fairy Castle Vent site: 1 spm (Figure 15o). Axial Seamount, Ashes vent field: - ROPOS R406, 10 spms (FMNH 280889).

Distribution: JdF in 1500–2400 m depth.

Remarks: We have finally been able to examine specimens young enough to show the protoconch (Figure 15o), which is strongly ridged, like all the peltospirid limpet groups and *Lirapex*. This indicates that the genus belongs to that group of genera and not to the neomphalid radiation.

Subclass NERITIMORPHA

Superfamily NERITOIDEA Rafinesque, 1815

Remarks: Three endemic genera of Neritoidea have been reported from vents and seeps, *Bathynerita*, *Shinkailepas*, and *Olgasolaris* but their relations remain uncertain. *Bathynerita naticoidea* closely resembles Neritidae, and the only noteworthy anatomical difference from shallow water species of that family is the presence of cephalic lappets in *Bathynerita*. Their presence is, however, probably plesiomorphic since such lappets occur in most vetigastropod taxa and since the penis of male *Bathynerita* is a modified such lappet. A very similar penis is present in all Neritoidea and we believe they have lost the lappets.

The two limpet-shaped genera *Shinkailepas* and *Olgasolaris* appear quite different, and Beck (1992b) assumed *Olgasolaris* to have “been adapted to hydrothermal vents for a very long time” (contrasting *Shinkailepas*). McArthur & Tunnicliffe (1998) considered *Olgasolaris* to be phylogenetically close to *Nerita*, while *Shinkailepas* and *Bathynerita* were believed to form a more distant group.

A problem in the assessment of relations is that little is known about Neritopsidae, the second main group of Neritopsina. Their radula has lost most of the central field (Warén & Bouchet, 1993), as in Titiscaniidae, and is of little use for comparative purposes. We have seen no protoconchs of *Neritopsis* good enough to allow comparison with *Shinkailepas*, and the soft parts have not been de-

scribed in enough detail to allow comparison (only a female described, Fischer 1875). Species of Neritopsidae live deep down in the interstices in coarse coral gravel and in submarine caves (Kase & Hayami, 1992).

The third group of Neritimorpha is better known (Fretter, 1984). Species of the family Phenacolepadidae usually live under buried, decaying wood, under rocks, or in subterranean tidal water passages in coral platforms where high bacterial activity can be expected from the presence of organic material and dissolved, reducing compounds (Fretter, 1984; Bouchet & Warén, 1993, unpublished observations). Due to this way of living, they are rarely found alive, and fresh shells of most species frequently are covered by or have remains of crusts of rust. An ability of the larvae to recognize these kinds of biotopes, as well as their use of hemoglobin as respiratory pigment, may have been a starting point for the evolution of taxa restricted to vents and seeps.

The radula of *Bathynerita* resembles that of shallow water neritids in the massive development of tooth number 5, while in *Olgasolaris* and *Shinkailepas* it is smaller with a few well developed cusps. This may, however, be caused by heterochrony since very young *Smaragdia* and *Nerita* have a small tooth number 5 with strong cusps (unpublished). When discussing the relations of *Olgasolaris* and *Shinkailepas*, Beck (1992b) commented that their outermost marginal tooth was “flabelliform as in Pleurotomariacea.” The latter statement needs some comments. Similar marginal teeth were considered typical for Eucyclinae (Trochidae, Trochoidea) by Hickman & McLean (1990:74, fig. 43F), but this kind of outer marginals, sometimes very broad (as in *Sutilizona pterodon*, Figure 18a), sometimes more slender (Figure 18g), seems to occur in most groups of vetigastropods, although they may be difficult to distinguish because they have a strong tendency to stick together (Warén, in press).

Olgasolaris has well developed cephalic lappets like *Bathynerita* and is in this aspect probably plesiomorphic, while *Shinkailepas* lacks them.

The shell characters of *Shinkailepas*, *Olgasolaris*, and Phenacolepadidae are difficult to use for classification since much homoplasy probably is involved in the process of limpetization. Nevertheless it should be noticed that the veliger larvae of *Shinkailepas* do resorb the internal coiling of the protoconch. So do also the species of Neritidae with both protoconch and teleoconch, while species of Neritopsidae do not resorb the early whorls.

This discussion can hardly be carried further until more anatomical information is available, which is beyond the

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Figure 31. Radulae. Teeth numbered sequentially with central tooth as 0. a–c. *Lirapex costellata* Warén & Bouchet, sp. nov., paratypes. a. Full width of radula. b. Detail of marginal teeth. c. Detail of central field. d. *Shinkailepas briandi* Warén & Bouchet, sp. nov., MAR, Menez Gwen. e, f. *Peltospira smaragdina* Warén & Bouchet, sp. nov., MAR, Menez Gwen. e. Central field and first marginal tooth. f. Whole width of radula. Scale bars in μm .

intentions of this paper, and we keep *Bathynerita* in Neritidae and *Olgasolaris* and *Shinkailepas* in Phenacolepadidae.

Family PHENACOLEPADIDAE Pilsbry, 1895

Shinkailepas Okutani, Saito & Hashimoto, 1989

Shinkailepas Okutani, Saito & Hashimoto, 1989:224.

Type species: *Shinkailepas kaikatensis* Okutani, Saito & Hashimoto, 1989; by original designation; hydrothermal vents at Kaikata Seamount, Japan.

Remarks: Beck (1992b) described a second species, *Shinkailepas tufari*, from hydrothermal vents at the Manus Back Arc Basin, and is in the process of describing a third species from the Fiji and Lau Basins. These species are all quite uniform in shell and soft part morphology and differ mainly in the position and development of the apex, size, and details in the shell sculpture.

Shinkailepas briandi Warén & Bouchet, sp. nov.

(Figures 16a, b, 31d, 32a–h, 33a–e)

Type material: Holotype and 8 paratypes in MNHN.

Type locality: MAR, Menez Gwen, DIVA 2 PL 26, 37°50.54'N, 31°31.30'W, 860–870 m.

Material examined: MAR, Menez Gwen: - DIVA 1 PL 13, 1 spm; on an active chimney, 24 spms + egg capsules; - DIVA 2 PL 12, 3 spms; - DIVA 2 PL 14, suction sample among mussels, 4 spms; - MARVEL PL1201, 850 m, 4 spms; - MARVEL PL1208, retrieval box, 5 spms. *Lucky Strike*: - DIVA 1 PL 01, among mussels, 23 spms + egg capsules; - DIVA 1 PL 03, 51 spms; - DIVA 1 PL 04, 2 spms; - DIVA 1 PL 08, on a rock, 55 spms; - DIVA 1 PL 17, 60 spms, among mussels, 3 spms; - DIVA 1 PL 18, among mussels, 5 spms; - DIVA 2 PL 1, 1 spm; - DIVA 2 PL 2, 429 spms; on chimney, 3 spms; on sulfide flange, 120 spms; - DIVA 2 PL 03, 1 spm; - DIVA 2 PL 04, 7 spms; - DIVA 2 PL 05, 7 spms; - DIVA 2 PL 07, 140 spms; on mussels, 26 spms; 3 suction samples among mussels and hydrothermal sediments, 1, 2 & 3 spms; - DIVA 2 PL 08, 32 spms; 2 suction samples among mussels and hydrothermal sediments, 1 spm each; - DIVA 2 PL 09, 12 spms; suction sample among mussels and hydrothermal sediments, 2 shs; - DIVA 2 PL 10, suction

sample among mussels and hydrothermal sediments, 1 spm; retrieval box, 1 spm; - DIVA 2 PL 19, 1 spm; - DIVA 2 PL 20, 1 spm; - DIVA 2 PL 23, 19 spms; - DIVA 2 PL 25, 381 spms; - DIVA 2, in particle trap, 1 spm; - ALVIN dive 2604, 4 spms + egg capsules; 1636 m, 1 spm; - ALVIN dive 2605, 39 spms + egg capsules; - ALVIN dive 2606, 48 spms + 1 veliger; - LUSTRE Exp. Sintra site, on mussels, 27 spms; - MARVEL PL1193, Tour Eiffel, retrieval box, 1 spm; - MARVEL PL1200, Bairro Alto, 0.25 m² rock surface close to edifice, 39 spms; - MARVEL PL1205, Bairro Alto, retrieval box, 8 spms; - MARVEL PL1206, retrieval box, 1700 m, 4 spms. *Snake Pit*: - ALVIN dive 2622 (Elan), 16 spms. *Rainbow*: - MARVEL, 3 particle traps, 2 veligers, 3 young. *MAR Logatchev site*: - MICROSMOKE PL 14, 8 spms; - MICROSMOKE PL 20 (Irina), 1 spm.

Distribution: The MAR, from Menez Gwen to Logatchev site, at a depth of 850–3500 m, on mussels and rocks.

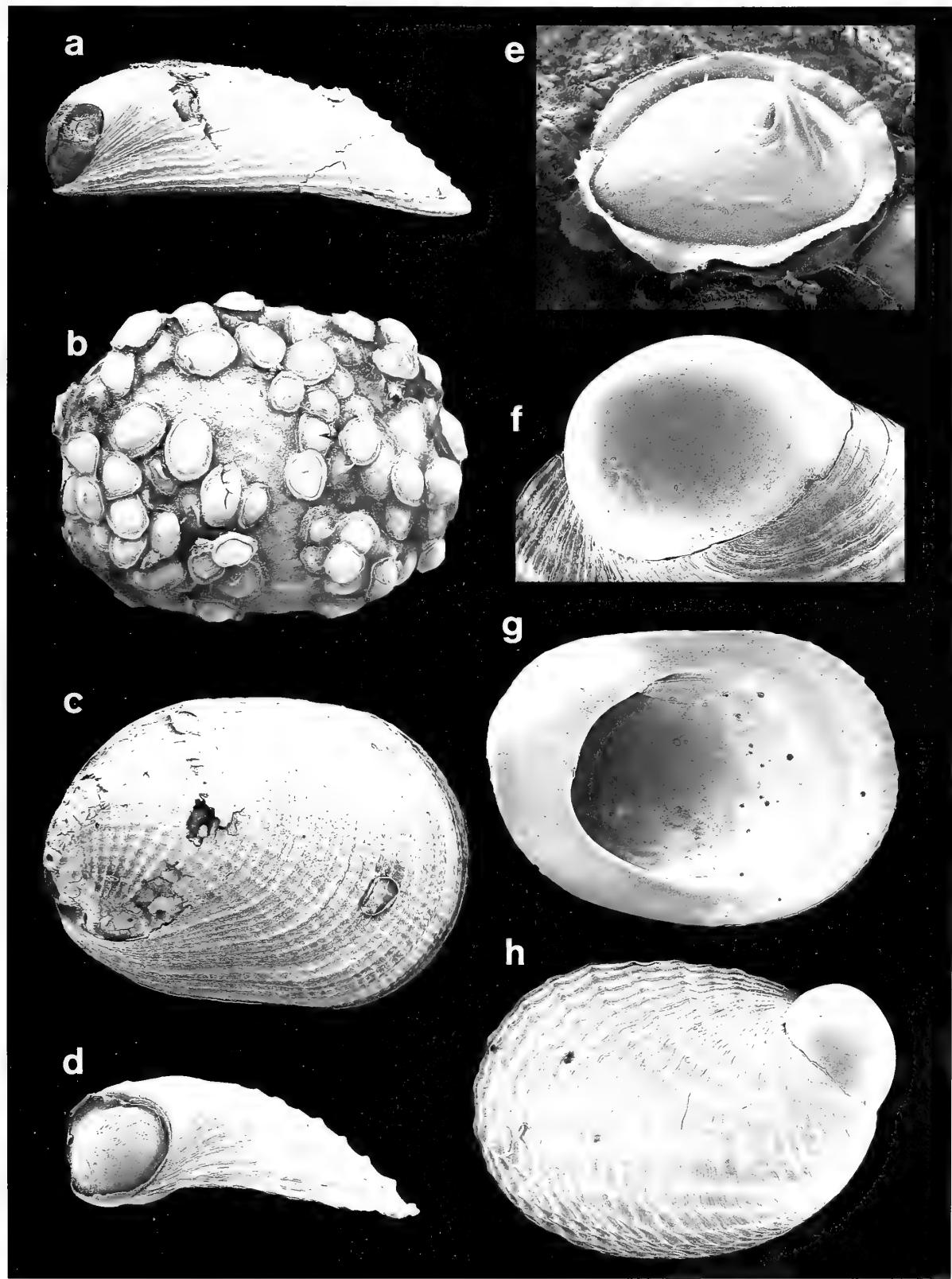
Etymology: Named after Patrick Briand at IFREMER, who has sorted much of the material from the French deep-sea program.

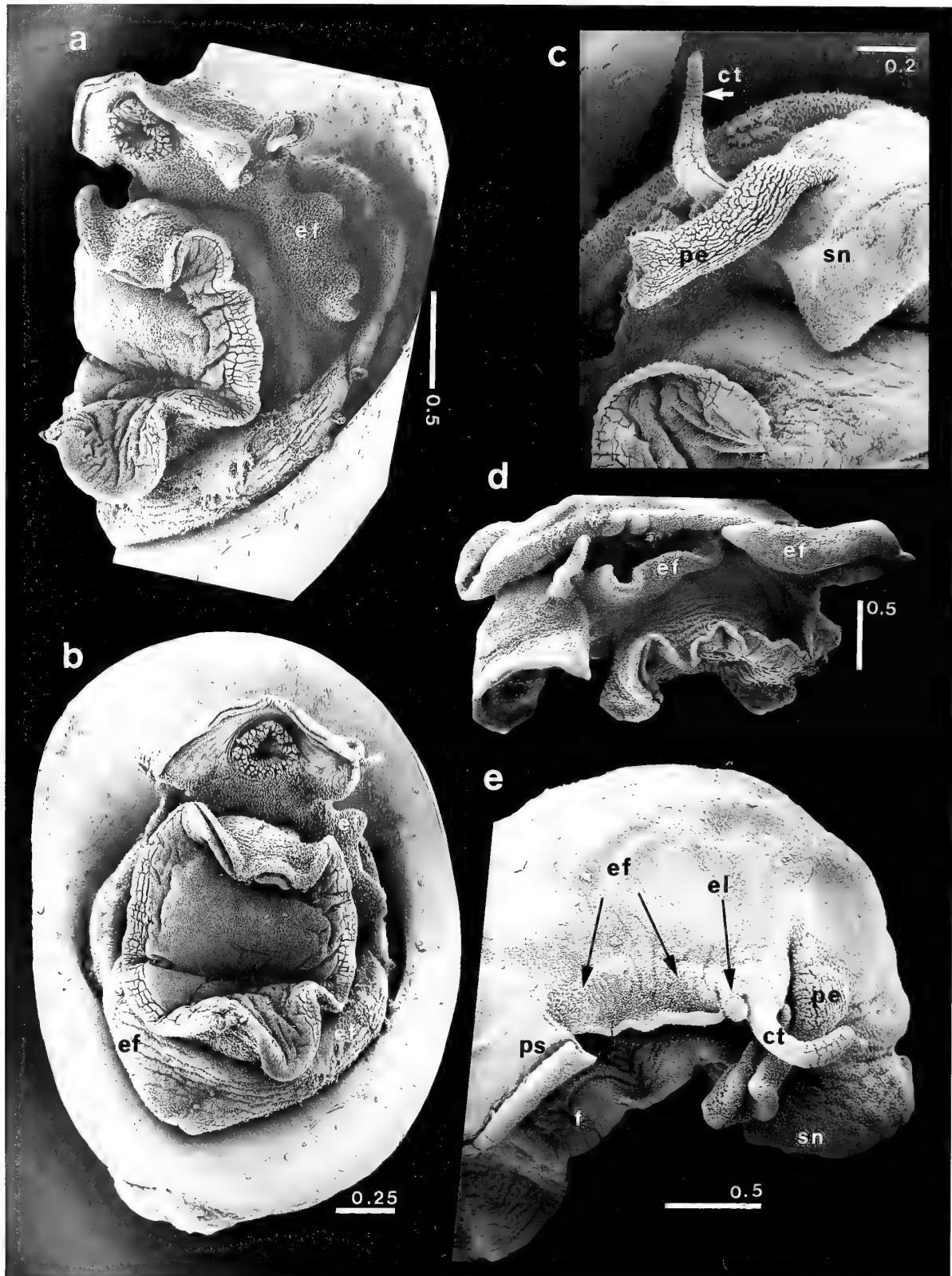
Description: *Shell* (Figures 32a–d, g, h). Limpet-shaped, ovate, low, rather sturdy, covered by a thin colorless periostracum, with distinct columellar shelf and apex situated straight above this. The protoconch (Figure 32f) is small and smooth with slightly expanded peristome; earlier whorls concealed by later ones, except a part of protoconch 1. Diameter 750–800 µm. The teleoconch consists of slightly more than one whorl, with the small spire situated at the posterior right ¼. The sculpture consists of collabral, low lamellae and numerous spiral ridges which are crossed by the lamellae. The columellar shelf is wide, corresponding to ca. ½ of the length of the shell. The muscle scars are situated, one at each side, under the most anterior part of this shelf; they are as long as high and their length corresponds to ¼ of the shell. The shell margin is not thickened.

Dimensions. Holotype, maximum diameter 8.9 mm, average adult size 5 mm, maximum size 10 mm.

Soft parts (Figures 33a–e). The foot is low and flat, anteriorly truncated with rounded corners and a propodium demarcated by a fissure. The epipodium consists of a simple flat ridge or skin fold which encircles the foot, from the left to the right cephalic tentacle base. Its posterior part is thick and folded and can probably be expanded to cover the whole columella and shell margin,

Figure 32. *Shinkailepas briandi* Warén & Bouchet, sp. nov., MAR. a. Adult specimen, Lucky Strike, lateral view, 5.6 mm. b. Adult specimen covered by egg capsules, Menez Gwen, diameter of shell 6.0 mm. c. Large shell, Menez Gwen, diameter 8.4 mm. d. Young specimen, protoconch corroded, Lucky Strike, diameter 1.9 mm. e. Egg capsule, Menez Gwen, diameter, 0.77 mm. f. Protoconch, Lucky Strike, diameter of shell 0.78 mm. g. Adult shell, apertural view, Lucky Strike, diameter 4.9 mm. h. Young specimen with preserved protoconch, Lucky Strike, diameter of shell 2.2 mm.





as indicated by their smooth surface. The neck-lobe is not demarcated from the epipodium. The operculum is not visible from the outside but lies in a deep pocket between the epipodium and the visceral mass. The head is very large and broad, the snout even wider and drawn out to lateral flaps. The mouth is ventral and surrounded by a fringe of large papillae. The cephalic tentacles are long and slender, tapering, and have a small, basal eye-lobe, but no externally visible eye (except in the veligers). The male has a large, gutterlike penis attached anteriorly to the tentacle. The gill is large, bipectinate, lacks sensory bursicles, and is attached only very basally.

Egg capsules (Figure 32e). The capsules are tough and sturdy, maximum diameter 0.7–0.9 mm, and contain 5–13 eggs of a diameter of 90–100 µm. Veligers ready to hatch have a diameter of 125–135 µm. Recently laid capsules are transparent, older ones brownish opaque.

Operculum (Figures 16a, b). The operculum is irregularly shaped, rather thin, patchily calcified. The larval operculum is readily distinguished at the apex, partly surrounded by later growth. It consists of a small, smooth initial part, probably corresponding to the operculum of the hatching larva, diameter ca. 110 µm; then follows ¾ spirally striated whorl, corresponding to the planktotrophic life, diameter 0.55–0.60 mm. At this stage the operculum has a ridgelike muscle attachment with a small lateral peg on the inside (Warén & Bouchet, 1993:fig. 1d). The part formed during the benthic life is thin and fragile, sculptured with distinct growth lines. The length corresponds to about ⅓ of the length of the shell.

Radula (Figure 31d). n - 4 - 1 - 4 - n. The central tooth is a low, rectangular plate, slightly expanded apically and with one or two transverse ridges. The first lateral looks like a pair of parallel lamellae, which are joined at the outer extreme part. Lateral tooth number two is slightly smaller than the rhachidian, very irregular and shapeless with a “double” apical triangular plate, and a strong posterior supporting ridge. The third lateral tooth is simple, rounded, and scalelike, about twice the size of number 2. Lateral tooth four is large and robust, with a large, sturdy triangular apical plate which is weakly serrated at the inner edge. The outer supporting ridges, posterior and anterior ones, are fused to a large shield which forms a demarcation to the marginals. The inner marginal teeth are shorter than the outer lateral one, slightly longer toward the edge, flat, densely packed. The inner marginal teeth have a tricuspidate apical plate; farther toward the edge the cusps are more numerous and much smaller.

Remarks: The size of the veligers ready to hatch (125–

135 µm) and the size of the recently settled larvae, maximum diameter 0.8 mm, clearly shows that the larvae pass through a planktotrophic phase. The soft parts of the newly settled larva are brightly pigmented with black, and the larva has eyes. The visceral mass is not coiled, but forms a round sac, because the interior of the whorls are resorbed also in the protoconch.

Shinkailepas briandi is one of the most common gastropods from the better investigated localities at the MAR. The veliger larva resembles that of *Smaragdia viridis* (Linnaeus, 1758) (Neritidae) in size and shape. Larvae of *Smaragdia* have, however, an opercular sculpture by growth lines only, no spiral lines.

Family NERITIDAE Rafinesque, 1815

Bathynerita Clarke, 1989

Bathynerita Clarke, 1989:125.

Type species: *B. naticoidea* Clarke, 1989; by original designation; Caribbean hydrocarbon seeps.

Taviani (1994) mentioned that, based on unpublished data, he considered *Thalassonerita* Moroni, 1966 a senior synonym of *Bathynerita*.

Bathynerita naticoidea Clarke, 1989

(Figures 30d–f)

Bathynerita naticoidea Clarke, 1989:125, figs. 3, 4; text figs.

Bathynerita naticoidea: Warén & Bouchet, 1993:3, figs. 1, 2, 3A–C.

New records: Off Louisiana: - Johnson Sealink dive 3129, 200 spms. Off Barbados (El Pilar Sector): - DIAP-ISUB 15-2, 35 spms.

Distribution: Recorded from five localities at 27°41–47'N, 91°13–30'W, 550–800 m depth (Zande, 1994); herein also from off Barbados, 11°14'N, 59°30'W, 1135 m.

Remarks: The ecology of *Bathynerita naticoidea* was studied by Zande (1994), who found no bacterial symbionts, only scattered fungi on the gill, and concluded that the main diet is chemosynthetically nourished macrofauna and flora obtained by scraping hard surfaces. She concluded that the development is lecithotrophic, but this was not clearly shown and we favor the opinion that the development is planktotrophic. The egg capsule is figured in Figure 30f and is of normal neritoid morphology (Neritidae: Andrews, 1935; Phenacolepadidae: Risbec, 1935, figs 6–8, as *Cocculina* sp.). Our egg capsules have a diameter of ca. 1.2 × 0.9 ± 0.2 mm and contain about 25–

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Figure 33. *Shinkailepas briandi* Warén & Bouchet, sp. nov., MAR, critical-point dried. a. Left side of body. b. Ventral view. c. Right side of head. d. Left side of body. e. Left side of head. ct - cephalic tentacle; ef - epipodial fold; el - eye-lobe; f - foot; pe - penis; ps - pallial skirt; sn - snout. Scale bars in mm.

35 eggs of a diameter of 90–100 µm which develop to veligers of a shell diameter of 130–140 µm (Figures 30d, e). Eckelbarger & Young (1997) investigated the oogenesis, and reported a maximum egg diameter of 135–145 µm, but this may refer to eggs flattened by deformation and compression in the gonad. Zande (1994) reported egg capsules of twice this size with 130–180 embryos of similar diameter. The measurements correspond well with the size of protoconch 1 of *Nerita atramentosa* Reeve, 1855, from Australia (own observation), *Neritina virginea* (L., 1758), *N. clenchi* (Russell, 1940), and *Nerita tessellata* Gmelin, 1791 (all Caribbean; Bandel, 1982). All these species are known to have planktotrophic development. Regrettably no benthic stages of *B. naticoidea* young enough to retain any trace of the protoconch have been seen by us (smallest specimen seen, 3.5 mm shell diameter), but this agreement in size gives an indication of planktotrophy, while there is no data to support lecithotrophy. The size of egg capsules (up to 2.9 × 2.15 mm) and numbers of embryos (130–180) given by Zande (1994) indicate a large variation (cf. 25–35, above), but the numbers correspond to the calculated increase in volume from a capsule diameter of 1.2 mm to 2.1 mm and are probably correct, since also the maximum size of the specimens varied considerably (11–19 mm) between the localities investigated by Zande.

Specimens from the Bush Hill Seep often have the egg capsules attached to their shell, but capsules were also found on *Provanna sculpta*, *Cataegis meroglypta*, and other shells. About half of the egg capsules from dive 3129 were hatched.

Subclass CAENOGASTROPODA

Family PROVANNIDAE Warén & Ponder, 1991

Remarks: Species of Provannidae have been found in fossil cold seeps back to Late Jurassic – Early Cretaceous deposits of the Great Valley Group in California (Campbell, personal communication). It is interesting that also species of *Abyssochrysos* (Abyssochrysidae) occurred there, since they have been assumed to be related to Provannidae (Warén & Ponder, 1991). Abyssochrybrids have so far not been reported from recent vents or seeps, although they have recently been reported from younger fossil cold seeps (Middle Eocene, State of Washington: Goedert & Kaler, 1996). Some caution is suggested about these records since the specimens are either poorly preserved, and no protoconchs have been examined, or the reports are preliminary.

Provanna Dall, 1918

Provanna Dall, 1918:7.

Type species: *Trichotropis* (?) (*Provanna*) *lomana* Dall, 1918a; by monotypy; deep water off southern California.

Remarks: The new material of species of *Provanna* is of great interest since it adds considerably to the distribution of six species and reduces the initial impression that every new locality had its own set of species. This is also the first time that species of *Provanna* have been recorded from a biogenic substrate (*P. macleani* and *P. pacifica* on sunken driftwood).

It is very rare to find anything left of the protoconch in species of *Provanna*, and we want to draw the attention to Gustafson & Lutz's (1994, fig. 4:14) figure of a well preserved protoconch of *Provanna variabilis*.

Provanna lomana (Dall, 1918)

Trichotropis (*Provanna*) *lomana* Dall, 1918a:7.

Provanna lomana: Warén & Bouchet, 1986:161, figs. 1, 2, 18, 23.

New records: *Oregon Margin*: - TVG 115, from calcareous blocks, 2 spms, 5 shs; - ROPOS #339, Pete Vent Field, 17 spms; - ROPOS #339, 9 shs (SMF 311993); - TVG 11, 2 shs, 4 spms (SMF 311994, 311995).

Distribution: From southern California to the Oregon Margin, ca. 450–1200 m.

Remarks: Examination of the soft parts and the radula did not reveal any difference between specimens from southern California and the Oregon Margin.

Provanna goniata Warén & Bouchet, 1986

Provanna goniata Warén & Bouchet, 1986:163, figs. 5, 6, 19, 25.

New records: *Guaymas Basin*: - GUAYANAUT PL 07, 1 spm; - GUAYANAUT PL 08, 1 spm; - GUAYANAUT PL 15, 8 spms; - GUAYANAUT PL 16, 13 spms; - GUAYANAUT PL 18, 28 spms.

Distribution: Only known from the Gulf of California, Guaymas Basin, 2020 m.

Remarks: This is the largest known species of *Provanna* with a shell height of up to 16 mm.

Provanna ios Warén & Bouchet, 1986

Provanna ios Warén & Bouchet, 1986:162, figs. 8, 9, 20, 22.

New records: *EPR at 13°N*: - HERO 91 PL 21, 1 spm; - HERO 92 dive 2517, 2 spms. *EPR at 17°S*: - NAUDUR PL 06, site Rehu, 3 spms.

Distribution: EPR from 21°N to 17°S, in 2450–2600 m depth.

Provanna laevis Warén & Ponder, 1991 (Figure 6c)

Provanna laevis Warén & Ponder, 1991:53, figs. 3C–D, 4A, 20H–I, 21C–D, 23D.

New records: JdF, Axial Seamount, Ashes vent field: - ROPOS R406, 25 spms (FMNH 280891). *Oregon Margin:* - ROPOS #339, Pete Vent Field, 7 spms (3 with *Pyropelta corymba* attached), 3 shs; with no detail, 1 spm, 5 shs; - TVG 11, 2 spms (1 with *P. corymba*) (1 in SMF 311996). *Guaymas Basin:* - GUYANAUT PL 13, 28 spms; - GUYANAUT PL 15, 3 spms; - GUYANAUT PL 16, 4 spms; - GUYANAUT PL 18, 44 spms, 14 shs.

Distribution: Gulf of California, Guaymas Basin, ca. 2000 m depth, to the Oregon Margin, 500–600 m depth and JdF, Ashes vent field, ca. 1500 m.

Remarks: Examination of the soft parts and the radula did not reveal any difference between specimens from the three widely separated localities mentioned above. Several specimens from the Oregon Margin had the cocculiniform *Pyropelta corymba* (see above) attached to the shell, and it is worth noticing that *Provanna laevis* was described from the same seep field in the Guaymas Basin as *P. corymba*, and later was recorded (McLean, 1992b: 409) from the type locality of *P. laevis*.

Provanna sculpta Warén & Ponder, 1991

Provanna sculpta Warén & Ponder, 1991:53, figs. 3A–B, 8, 14, 18, 20C, E, 21A–B, 23B.

New records: Off Louisiana: Johnson Sealink dive 3129, 45 spms, 21 shs.

Distribution: Only known from off Louisiana, at the Bush Hill Seep, at a depth around 550 m.

Remarks: Two shells had damaged outer lip, typical for crab predation. About half of the specimens had up to eight neritid egg capsules attached to the shell, and three specimens had very young *Bathymodiolus* sp. attached to shell.

Provanna variabilis Warén & Bouchet, 1986

Provanna variabilis Warén & Bouchet, 1986:163, figs. 13–15, 26–28.

Provanna variabilis: Gustafson & Lutz, 1994:figs. 4:13–15.

New records: Endeavour Segment: - ATV 50-1, Fairy Castle edifice, 1 spm. *Oregon Margin:* - ALVIN dive 2796-2927, 9 spms (Tunnicliffe).

Distribution: JdF, Oregon Margin at 45°N, and the Gorda Ridge (Gustafson & Lutz, 1994), at 675–2200 m depth.

Remarks: Gustafson & Lutz (1994) figured the protoconch, which seems to be the only known, well preserved protoconch of a species of *Provanna*.

Provanna macleani Warén & Bouchet, 1989

Provanna macleani Warén & Bouchet, 1989:94, figs. 111–114.

New records: *Oregon Margin:* - 44°40'N, 125°33'W,

2750 m depth, 2 spms from a piece of sunken driftwood (FMNH 278325).

Distribution: Previously only known from the type locality, 44°52.4'N, 126°40.8'W, 2713 m depth, near the new record.

Remarks: This is not a record that belongs to the vent fauna, but it is of interest because the habitat was not known for this and the following species, and they are the first documented records of the genus outside vent and seep environments.

Provanna pacifica (Dall, 1908)

Cerithioderma pacifica Dall, 1908a:324.

Provanna pacifica: Warén & Bouchet, 1986:161, figs. 4, 17.

New records: *Oregon Margin:* - 44°40'N, 125°33'W, 2750 m depth, 4 spms from a piece of sunken driftwood (FMNH 278325).

Distribution: Previously only known from the type locality, Gulf of Panama, 07°05.5'N, 79°40'W, 2311 m.

Remarks: See *P. macleani*.

Provanna sp. 1

Material examined: Edison Seamount: - 66-GTVA, 6 shs.

Distribution: Only known from this locality.

Remarks: Six shells of variable quality were found, but they are not good enough to be sure that they represent only one species and we refrain from describing it (them?).

Provanna sp. 2

Material examined: Aleutian Trench, Shumagin site: - TVGKG 40, 1 sh, 1 spm (SMF 311992).

Distribution: Only known from this locality.

Remarks: This is certainly an undescribed species, but the specimens are young, and premature description may cause future problems.

Provanna sp. 3

Material examined: Mid America Trench, Jalisco Block Seeps at 20°N: - NAUTIMATE PL 10, 2 shs.

Distribution: Only known from this locality.

Remarks: Two shells resemble *P. macleani* in lacking axial sculpture, but have weaker spiral ribs and a taller spire. This is certainly an undescribed species, but the specimens are young and a formal description would be premature.

Family CERITHIOPSIDAE H. & A. Adams, 1853

Remarks: The family Cerithiopsidae is not very well known and its systematics even less understood. It comprises numerous species, as far as known spongivorous. A review of the family is presently being prepared by Bouchet & Warén.

Speculator Warén & Bouchet, gen. nov.

Type species: *Speculator cariosus*, sp. nov.

Diagnosis: Shell tall, of a general “*Cerithiella* appearance” with rounded, convex whorls, obliquely drawn-out siphonal canal; no basal-central spiral thread. Radula with seven rows of low, sturdy teeth with three to several cusps.

Etymology: “*speculator*” (Latin) means “explorer,” alluding to the type species originating from the Explorer Ridge.

Remarks: The shell has a very generalized appearance for the family, but differs from *Eumetula* by lacking the basal thread typical for this genus, and by having undifferentiated lateral and marginal teeth in the radula. In *Eumetula* Thiele, 1912, the two marginals are tall, have a shaft, and are folded over the lateral tooth. *Speculator* superficially resembles species of *Cerithiella* Verrill, 1882, which also lack a basal thread but differ in having a longer, more curved siphonal canal and a different radular morphology with clawlike marginals (Bouchet & Warén, 1993:figs. 1273–1276).

The radula of *S. cariosus* is unusual in having a strong variation in the thickness and length of the cusps of the lateral and marginal teeth; these are usually quite uniform. It can only be speculated that this difference is caused by a change in diet in *S. cariosus* compared to other cerithiopsids. It was not possible to check the contents of the intestine, because we had to dry the soft parts in order to detach them from the columella, and rehydration afterward did not soften the body enough for dissection.

Speculator cariosus Warén & Bouchet, sp. nov.

(Figures 34c, d, 36c, 49g)

Type material: Holotype in MNHN.

Type locality: JdF, Explorer Ridge: Magic Mountain,

Steve 4 vent, ROPOS #284, 49°45.53'N, 130°15.50'W, 1762 m.

Material examined: Only known from the holotype.

Distribution: Only known from the type locality.

Etymology: “*cariosus*” (Latin) referring to the decaying appearance of some of the cusps of the radular teeth.

Description: *Shell* (Figure 34c). Tall, slender, rather fragile, brownish yellow, with reticulate sculpture. The apical whorls have been lost by corrosion; slightly more than seven distinctly convex whorls remain, sculptured by ca. 30 slightly curved axial ribs on the body whorl. The axial ribs are of varying strength and to some extent intergrading with the incremental lines, less so on the upper whorls. The spiral sculpture consists of four strong cords on the exposed part of the spire whorls and two more basal cords on the last whorl (Figure 34d), encircling the base. Scattered and indistinct, much finer striae are occasionally present above and below these cords. The outer lip is evenly curved, not thickened, and goes smoothly over into the short but very distinct canal.

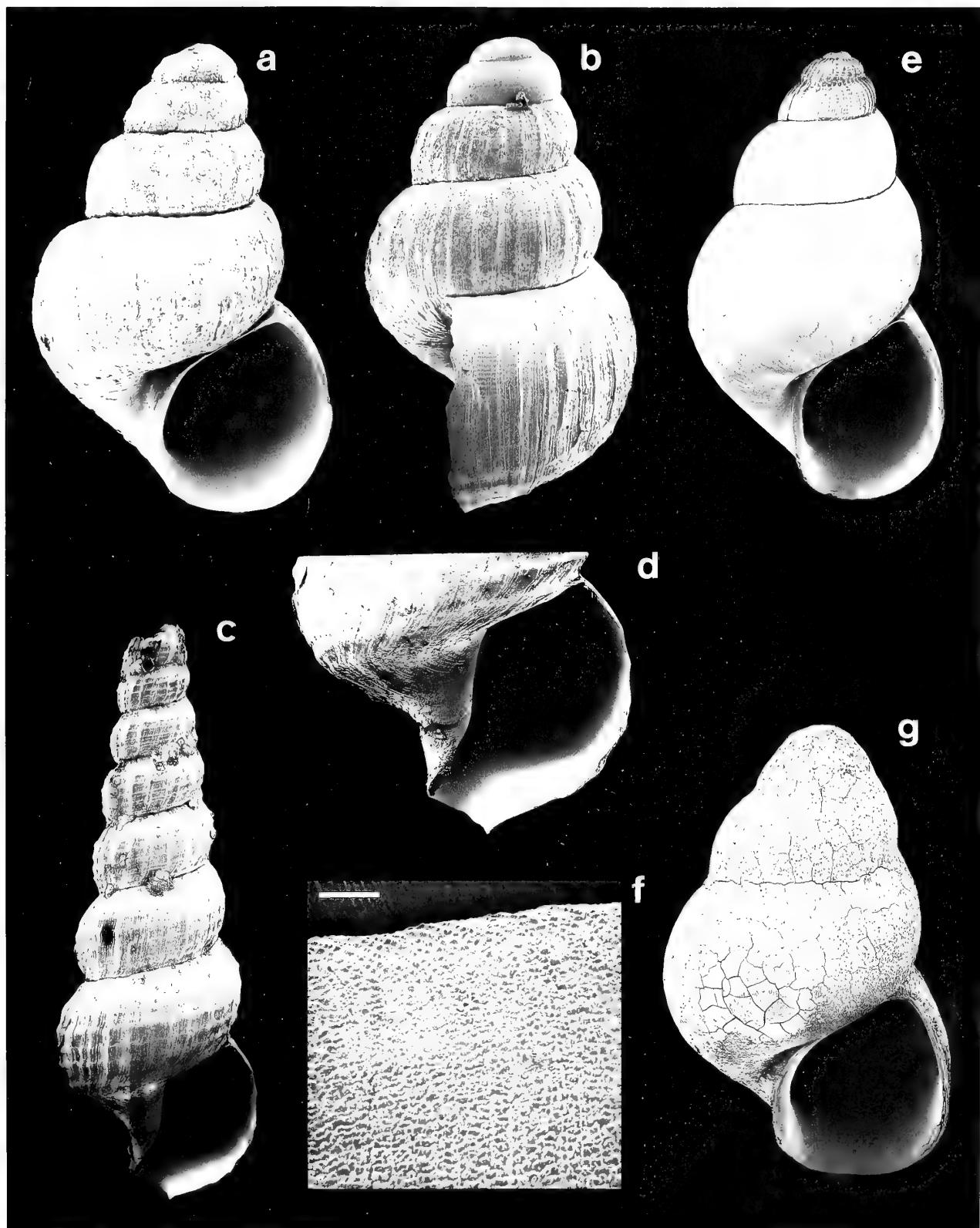
Dimensions. Height of shell 8.1 mm (apex missing), total height, estimated 8.3 mm.

Operculum (Figure 49g). It is thin, yellowish, paucispiral with indistinct coiling and strongly eccentric nucleus.

Radula (Figure 36c). Long and slender, with seven longitudinal rows of uniformly shaped teeth. Several cusps are in a process of becoming filamentous. The central tooth is very sturdy, low, and broad with three strong cusps of equal size and a smaller denticle at each side. The lateral and first marginal tooth are of very similar shape and their inner end has two well developed cusps of which the inner one is half the size of the one next to it. Then follows a series of about nine cusps of which the innermost is long, thin, and filiform; the following ones gradually increase in size so that the outer three cusps may be of the same width as the second inner cusp. There is, however, variation in this, and some teeth have no sturdy outer cusps, others have three, also in the same longitudinal row. Also the outer marginal tooth is similar, but here the sequence of the sturdy and variable cusps is inverted, so that the outer two or three cusps (often with a small denticle between the two outer ones) are sturdy and the inner teeth variable.

Remarks: As far as known, all species of Cerithiopsidae feed on sponges (Bouchet & Warén, 1993). This speci-

Figure 34. a, b. *Alvania cf. stenolopha*, Menez Gwen, 2.6 and 2.3 mm. c, d. *Speculator cariosus* Warén & Bouchet, gen. & sp. nov., holotype, height 8.5 mm. e-g. *Laeviphipitus desbruyeresi* Warén & Bouchet, sp. nov., Lucky Strike. e. Cleaned shell, height 1.84 mm. f. Detail of sculpture. g. Shell with normal ferruginous deposits, height 1.52 mm. Scale bar 20 µm.



men came from a grab with tube worms and no sponges in the vicinity. It seems thus possible that the species has another diet, which may be the reason for the strange appearance of the radula with some almost filiform denticles. Perhaps this is a case of recent immigration to the vent environment at the species level.

Family ELACHISINIDAE Ponder, 1985

Laeviphitus van Aartsen, Bogi & Giusti, 1989

Laeviphitus van Aartsen, Bogi & Giusti, 1989:20.

Type species: *L. verduini* van Aartsen, Bogi & Giusti, 1989; by original designation; upper bathyal, Mediterranean.

Remarks: The genus *Laeviphitus* was first known (but not described) from the characteristic veliger larvae (see Warén et al., 1990) which had been caught as plankton in the Mediterranean. A second species was reported as "unidentified veliger" by Turner et al. (1985: fig. 19) from bottom plankton at the Galapagos Rift Zone, and again by Mullineaux et al. (1996) from plankton samples taken a few meters above the sea floor at EPR, 09°50'N. Finally Okutani et al. (1993) described a species from a seep assemblage at the Kaikata Seamount (west of Ogasawara, Japan) at a depth of about 450 m. From the radular morphology they concluded that nothing contradicted a systematic position in the Elachisinidae (suggested by Warén et al., 1990), while a placement in the Epitonidae, as suggested in the description of the genus, was untenable. Still, the anatomy of *Laeviphitus* has not been examined and the systematic position remains uncertain.

The genus is easy to recognize when the surface deposits of bacterially precipitated iron and manganese oxides has been removed (e.g., by treatment with alkaline hydrogen peroxide or commercial bleach; *caution!* this will also damage the soft parts). The strongly cancellate protoconch, combined with a smooth, rissoiform teleoconch are unique.

Laeviphitus desbruyeresi Warén & Bouchet, sp. nov.

(Figures 34e–g, 36a, 37b, 49e)

Type material: Holotype and 22 paratypes in MNHN.

Type locality: MAR, Lucky Strike, DIVA 2 PL 07, Tour Eiffel, 37°17.32'N, 32°16.51'W, 1685 m.

Material examined: Menez Gwen: - MARVEL PL1208, 850 m, retrieval box, 1 spm; - MARVEL PP50, particle trap, 1 protoconch. Lucky Strike: - DIVA 1 PL 01, 3 spms; - DIVA 2 PL 06, 1 spm; - DIVA 2 PL 07, 3 suction samples among mussels and hydrothermal sediments, 17, 5, and 2 spms; - DIVA 2 PL 08, retrieval box, 1 spm, suction sample among mussels and hydrothermal sedi-

ments, 2 spms; - ALVIN dive 2607, 1 spm; - LUSTRE Exp. Sintra site, on mussels, 2 spms (no teleoconch); - MARVEL PL1191, Bairro Alto, suction sample, 1 spm.

Distribution: From Menez Gwen, Lucky Strike, and Rainbow, 850–2300 m depth, among mussels and in sediment.

Etymology: Named after D. Desbruyères, co-ordinator of the European AMORES program of exploration of the Mid-Atlantic Ridge.

Description: *Shell* (Figures 34e, g). Small, not especially fragile, rissoiform, smooth, usually covered by thick crusts (Figure 34g), with a distinctly demarcated and cancellate protoconch (Figure 37b). The protoconch 1 consists of an initial whorl which was corroded in the specimens examined and measures about 110 µm in diameter. Protoconch 2 consists of about 2.2 whorls and is sculptured by ca. 40 strong, curved axial ribs and nine or 10 spiral cords which are fused to the ribs but do not cross them and frequently are not perfectly aligned on the two sides of the rib. The diameter of protoconch 2 is ca. 400 µm. The teleoconch consists of 2.25–2.5 smooth whorls, connected by a shallow suture which is more conspicuous in cleaned specimens since there is an open fissure where the rust deposits have peeled off. There is no sculpture visible except very faint incremental lines on the minutely granular surface (Figure 34f). The peristome is bluntly rounded anteriorly, slightly pointed posteriorly, and the basal corner typical for elachisinids is poorly developed. Behind the inner lip is a narrow umbilical crevice.

Dimensions. Height of holotype 1.80 mm, maximum height 1.85 mm.

Operculum (Figure 49e). Thin, yellowish brownish, paucispiral.

Radula (Figure 36a). Taenioglossate. The central tooth is not very sturdy, M-shaped in apical view, with central and three smaller lateral denticles; no additional lower denticles, only a strongly projecting, narrow support. The lateral tooth is triangular, long, and slender with the central $\frac{1}{5}$ of the apical margin equipped with denticles, two to three smaller ones facing the center, a large one and about eight more lateral denticles. The main cusp is supported by a ridge. The first marginal is broad and flat, apically obliquely truncated, and serrated apically and along $\frac{1}{10}$ of the outer margin. The outer marginal tooth is half the width of the first and apically more rounded.

Remarks: *Laeviphitus desbruyeresi* differs from *L. verduini* mainly by its smaller size, ca. 2 mm (4 mm in *verduini*), and by being considerably more slender with flatter whorls. It differs from *L. japonicus* Okutani, Fujikura & Sasaki, 1993, by having a more evenly rounded peristome, especially the basal part, which is more typically shaped for the family in *L. japonicus*.

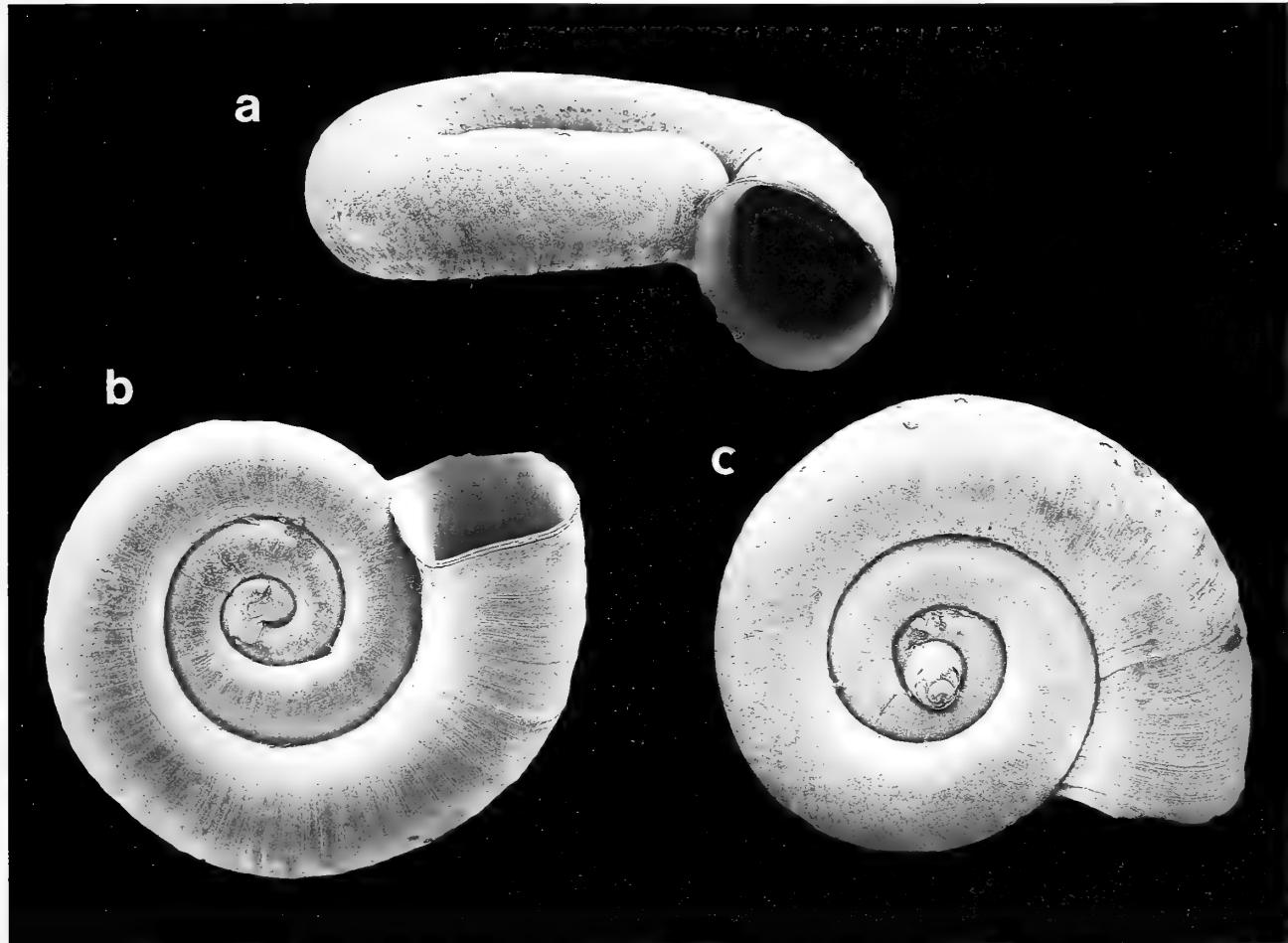


Figure 35. *a–c. Neusas* Warén & Bouchet, gen. nov., *marshalli*, MAR, Menez Gwen, diameter 2.06 mm.

Family VITRINELLIDAE Bush, 1897

Remarks: The family Vitrinellidae is presently not well understood, as is the case with the related Tornidae (for discussion see Ponder, 1994). Many species of the two families have a depressed to planispiral shell shape and a jaw similar to the new genus below (unpublished observations), and we have provisionally placed *Neusas* in the Vitrinellidae.

Neusas Warén & Bouchet, gen. nov.

Type species: *Homalogryra marshalli* Sykes, 1925.

Diagnosis: Small neotaenioglossate gastropods with more or less planispiral, slightly irregularly coiled teleoconch, strongly prosocline peristome, and a tall-spired, obliquely inserted protoconch. Operculum round, corneous, multispiral, with central nucleus. Radula 10 times as long as broad, taenioglossate, with very robust teeth. Central, lateral, and inner marginal tooth with strong irregularly shaped cusps often of alternating strength. Inner marginal

tooth very broad, triangular, and low. Outer marginal tooth simple, claw-shaped with three major cusps. Jaw sturdy with hexagonal pattern. Soft parts with pigmented, brownish zone from rear, left corner of pallial cavity, diagonally to just above head. Snout large, distally bilobed; cephalic tentacles small and inconspicuous, situated far apart, with small basal eyes at outer sides.

Etymology: From “*neuo*” (Greek), to lean one’s head, alluding to the inclined protoconch.

Remarks: We are not convinced that the type species belongs to the vent fauna, but take this occasion to make a new genus for a group of small, very rare gastropods. We have examined three similar species:

1. *Homalogryra marshalli*, treated here.
2. An undescribed, almost identical species from New Zealand, shells only (in National Museum of New Zealand).
3. An undescribed, less distinctly planispiral species from off New Caledonia, three specimens (in MNHN and

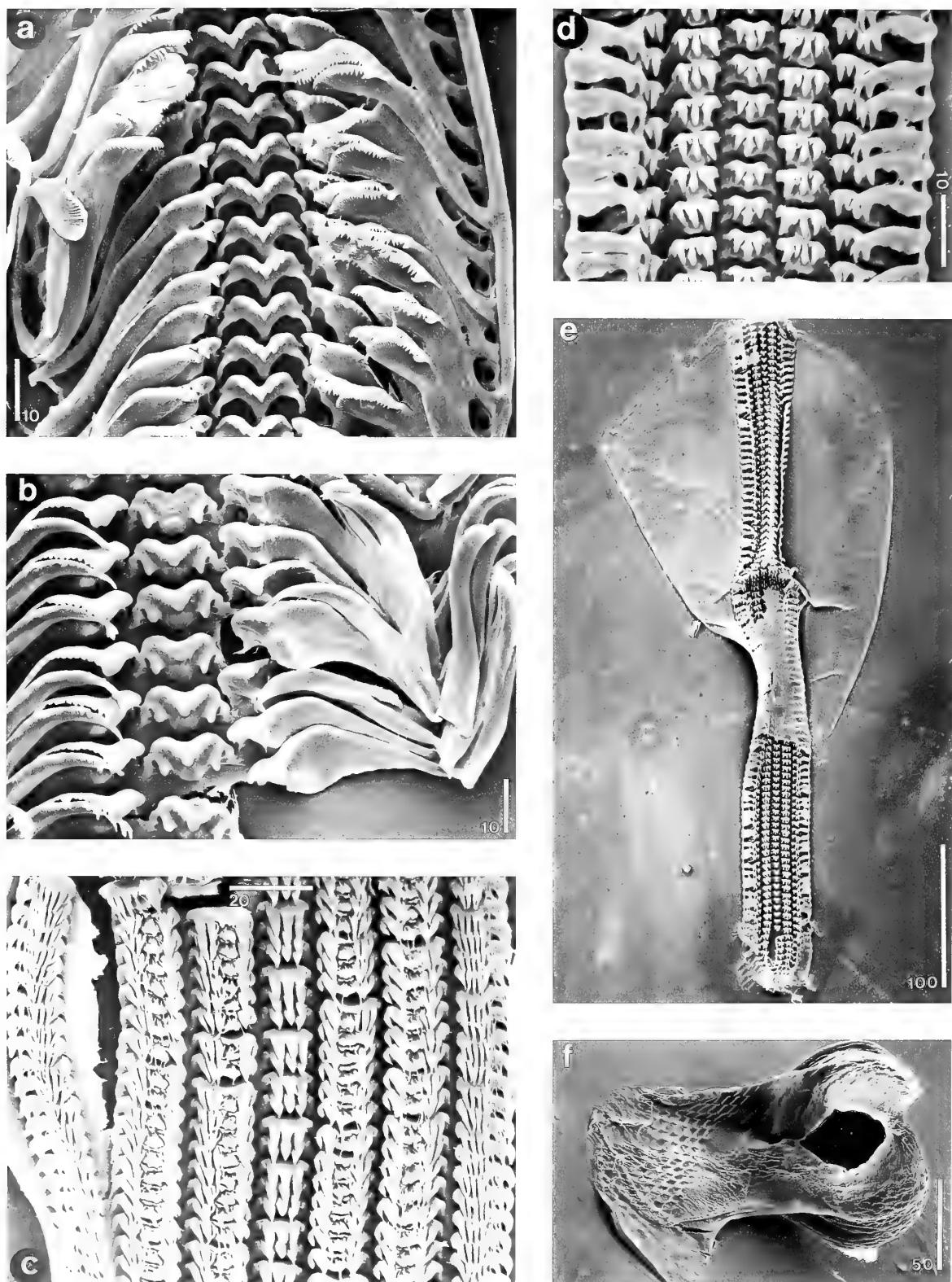


Figure 36. Radulae. a. *Laevipithitus desbruyeresi* Warén & Bouchet, sp. nov., MAR, Lucky Strike. b. *Alvania* cf. *stenolopha*, MAR, Lucky Strike. c. *Speculator cariosus* Warén & Bouchet, gen. & sp. nov., holotype. d-f. *Neusas* Warén & Bouchet, gen. nov., *marshalli*, MAR, Menez Gwen. d. Full width. e. Complete radula. f. Jaw. Scale bars in µm.

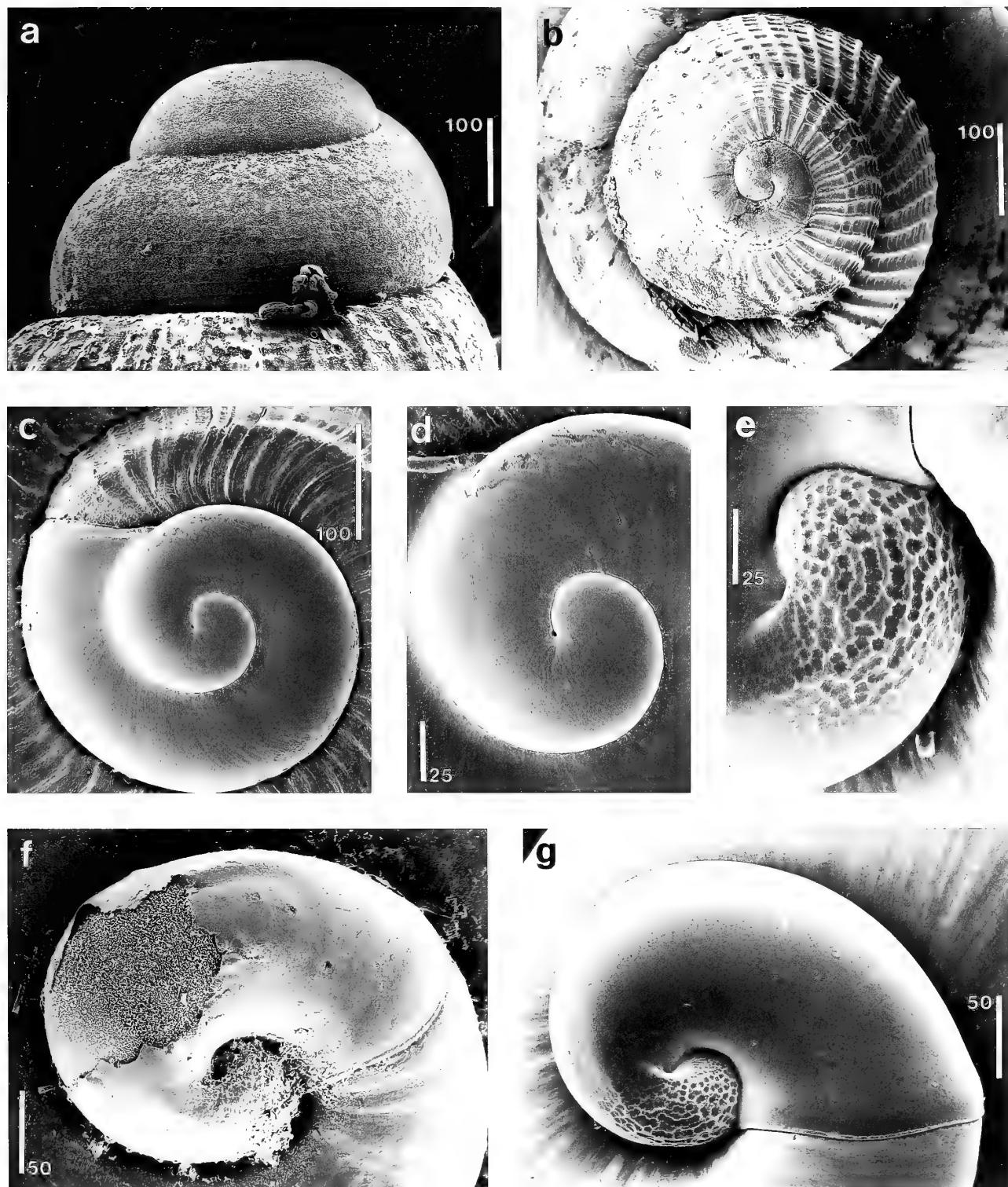


Figure 37. Protoconchs. *a*. *Alvania* cf. *stenolopha*, MAR, Lucky Strike. *b*. *Laeviphitus desbruyeresi* Warén & Bouchet, sp. nov., MAR, Lucky Strike. *c*, *d*. *Lurifax vitreus* Warén & Bouchet, gen. & sp. nov., MAR, Menez Gwen. *c*. Protoconch and first part of teleoconch. *d*. Detail of protoconch. *e*, *g*. *Hyalogyrina umbellifera* Warén & Bouchet, sp. nov., Aleutian Seeps, Shumagin site. *e*. Detail of initial whorl. *g*. Complete protoconch. *f*. *H. globularis* Warén & Bouchet, sp. nov., JdF, Endeavour Segment. Scale bars in μm .

Australian Museum, Sydney), of which one was used for examination of the radula after SEM of the shell.

Species 3 has an almost identical radula and jaw, in spite of being less distinctly planispiral, and the three are considered congeneric. The relation to other neotaenioglossate gastropods is uncertain but a few details give some clues.

-The teleoconch is evidently very modified and gives no hints.

-The protoconch has about 2.7 smooth and tall whorls and is well preserved in one of the specimens from New Caledonia.

-The structure of the jaw is not common among the Neotaenioglossa, but occurs in some species of Vitrinellidae (Ponder, 1994; own observations), and occurs also in a group of small species that can be typified by *Scrupus hyalinus* (Odhner, 1924) from New Zealand (also Vitrinellidae).

-The general style of the radula is most similar to the Littorinidae and Zerotulidae, which have a very long and slender radula, 20–50 times as long as broad. Also *Neusas* has a very high number of transverse rows of teeth, about 150.

The notes on the soft parts are based on the dried specimen and this information is obviously not enough to classify *Neusas*, but we have at present not wanted to use the remaining specimen of species 3 for anatomical work and leave the systematic position open. Vitrinellidae is in any case closer to the true systematic position than the original allocation of the species in the genus *Homalogryra* (Homalogryidae, "lower Heterobranchia").

Neusas marshalli (Sykes, 1925)

(Figures 35a–c, 36d–f, 49f)

Homalogryra marshalli Sykes, 1925:193, pl. IX, figs. 9, 9a.

Type material: Holotype in BMNH (examined).

Type locality: Porcupine Expedition 1870, station 17, off Portugal, 39°42'N, 09°43'W, 1092–1993 m.

New records: MAR, Menez Gwen: - DIVA 2 PL 26, 1 spm.

Distribution: Only known from the type locality and the new record, 850–2000 m.

Remarks: See "Diagnosis" of the genus for a redescription. The holotype is an empty shell, somewhat damaged, and our identification can be questioned. We have, however, not seen any additional species from the Atlantic and members the group are evidently very rare.

Family RISSOIDAE Gray, 1847

Remarks: The rissoids of the deep north-eastern Atlantic were recently revised (Bouchet & Warén, 1993) to which paper we refer for further discussions.

Alvania Risso, 1826

Alvania Risso, 1826:140.

Type species: *A. europaea* Risso, 1826; by subsequent designation by Nevill (1885:105); Mediterranean shallow water.

Alvania cf. *stenolopha* Bouchet & Warén, 1993

(Figures 34a, b, 36b, 37a)

Alvania stenolopha Bouchet & Warén, 1993b:653, figs. 1447, 1482–4.

New records: MAR, Menez Gwen: - DIVA 1 PL 16, on base of a black smoker, 1 spm; - DIVA 1 PL 14, on sulfide rock with Hydrozoa, 16 spms (decalcified). *Lucky Strike*: - DIVA 1 PL 04, on inactive chimney among Hydrozoa and sponge *Cladorhiza*, 1 spm; - DIVA 2 PL 02, 5 spms; - DIVA 2 PL 04, 1 spm; - DIVA 2 PL 09, 1 spm; - DIVA 2 PL 10, retrieval box, 3 spms; - ALVIN dive 2605, 1 spm; - ALVIN dive 2607, 17 spms, 1 egg capsule.

Distribution: MAR, 39.5–37.3°N, in 650–1850 m, probably epifaunal.

Remarks: The shell of this species seems unusually sensitive to formaldehyde and only a single shell was in good, but not perfect, condition. The species was described from two shells, from a place about 150 km NE of Menez Gwen at a depth of 650–1300 m. It is uncertain whether it is a member of the vent fauna or an occasional guest, but no other species which we know to occur outside vent areas was as frequent in samples dominated by "vent species," as *A. stenolopha*.

The egg capsule is spherical, with a transparent wall to which a few mineral grains are attached. It contains a single young ready to hatch and of the same size and structure (SEM) as the protoconch in our specimens, and the development is thus lecithotrophic.

Pseudosetia Monterosato, 1884

Pseudosetia Monterosato, 1884:281.

Type species: *Rissoa turgida* Jeffreys, 1870; by subsequent designation by Crosse (1885:140); northern Europe.

Pseudosetia azorica Bouchet & Warén, 1993

Pseudosetia azorica Bouchet & Warén, 1993:690, figs. 1603–4, 1615–7.

New records: MAR, Menez Gwen: - DIVA 2 PL 11, 3 spms.

Distribution: *Pseudosetia azorica* was described from three localities slightly farther to the east, on the southern slopes from the Azores, at a depth of about 350–850 m.

Remarks: We are not sure whether this is a species that belongs to the vent fauna, but since three specimens were found alive, and no details are known about the other localities from which it was described, we have included it here with a big question mark.

Family MURICIDAE Rafinesque, 1815

Trophon Montfort, 1810

Trophon Montfort, 1810:482.

Type species: *Murex magellanicus* Gmelin, 1791; by original designation; southern South America.

Remarks: The genus *Trophon* s.l. comprises numerous species with a northern or southern distribution, as well as in deep water (absent from shallow, warm water).

Trophon spp.

Material examined: Off Barbados (*Orenoque B and El Pilar Sector*): - DIAPISUB 10-4, 1 spm; - DIAPISUB 15-8, 1 spm; - DIAPISUB 16-3, 5 spms.

Remarks: Two species were present, one with a shell similar to *Trophon mucronae* Houart, 1991, from off Brazil, but with tall and slender protoconch. Species of *Trophon* usually are quite variable and we prefer to leave them undescribed, awaiting more material.

Family BUCCINIDAE Rafinesque, 1815

Remarks: Deep-sea buccinids in general were discussed by Bouchet & Warén (1986) and Lus (1989) and we refer there for some discussion of the group. Since then, several species have been recorded or described from hydrothermal vents, various kinds of seeps (Warén & Bouchet, 1993; Okutani et al., 1992, 1993; Okutani & Ohta, 1993) and whale skeletons (Naganuma et al., 1996, 1999), and it seems clear that members of the family are among the normal inhabitants in environments based on chemosynthetic activity. Buccinids belong to the gastropods known from the greatest depths, and *Callioncha iturupi* Lus, 1989, is the deepest described gastropod, from a depth of 8240–8345 m in the Kuril-Kamchatka Trench.

Bayerius Olsson, 1971

Bayerius Olsson, 1971:57.

Type species: *Fusinus fragilissimus* Dall, 1908; by original designation; deep water off Ecuador.

Tacita Lus, 1971:62. (New synonym)

Type species: *T. holosericea*, Lus, 1971; by original designation; abyssal, 6090–6135 m, in the Kuril-Kamchatka Trench (Holotype in the Institute of Oceanology, Moscow; Figures 38f, g).

Remarks: The shell and radula of the type species of

Bayerius and *Tacita* are so similar that there seems to be no reason for maintaining them as distinct genera. *Bayerius* was published March 1971; the volume of "Trudy Instituta Okeanologii" in which *Tacita* was described is dated 1971, and inquiries at the institute (through Dr. Y. Kantor) failed to produce a more precise date than this. We have therefore used the name *Bayerius*. *Callioncha* Lus, 1978 (type species *C. solida* Lus, 1978 from almost 7000 m in the Izu-Bonin Trench [= Japan Trench]) may be a third name for this genus, but we have not examined actual specimens.

Olsson (1971) recorded *Bayerius fragilissimus* from the Gulf of Panama, but the precise type of habitat is not known. Such is the case also with *B. holosericeus* and the original material of *B. arnoldi*. All records of the two latter species do, however, come from the East and North Pacific trenches (not more shallow than 2877 m). Probably the species are not obligate members of this fauna since it seems unlikely that dredging and trawling should have produced as much material as was known before the exploration of the seep systems. *Bayerius holosericeus* differs distinctly from *B. arnoldi* and *B. peruvianus* by having an evenly and deeply sinuated outer lip, while that of the two others is considerably straighter. We figure the holotype (Figures 38f, g).

Bayerius peruvianus Warén & Bouchet, sp. nov.

(Figures 38h, 39c, 49d)

Type material: Holotype and 12 paratypes in MNHN.

Type locality: Peru, off Paita, NAUTIPERC PL 18, 10°01'S, 80°07'W, 5996–5385 m.

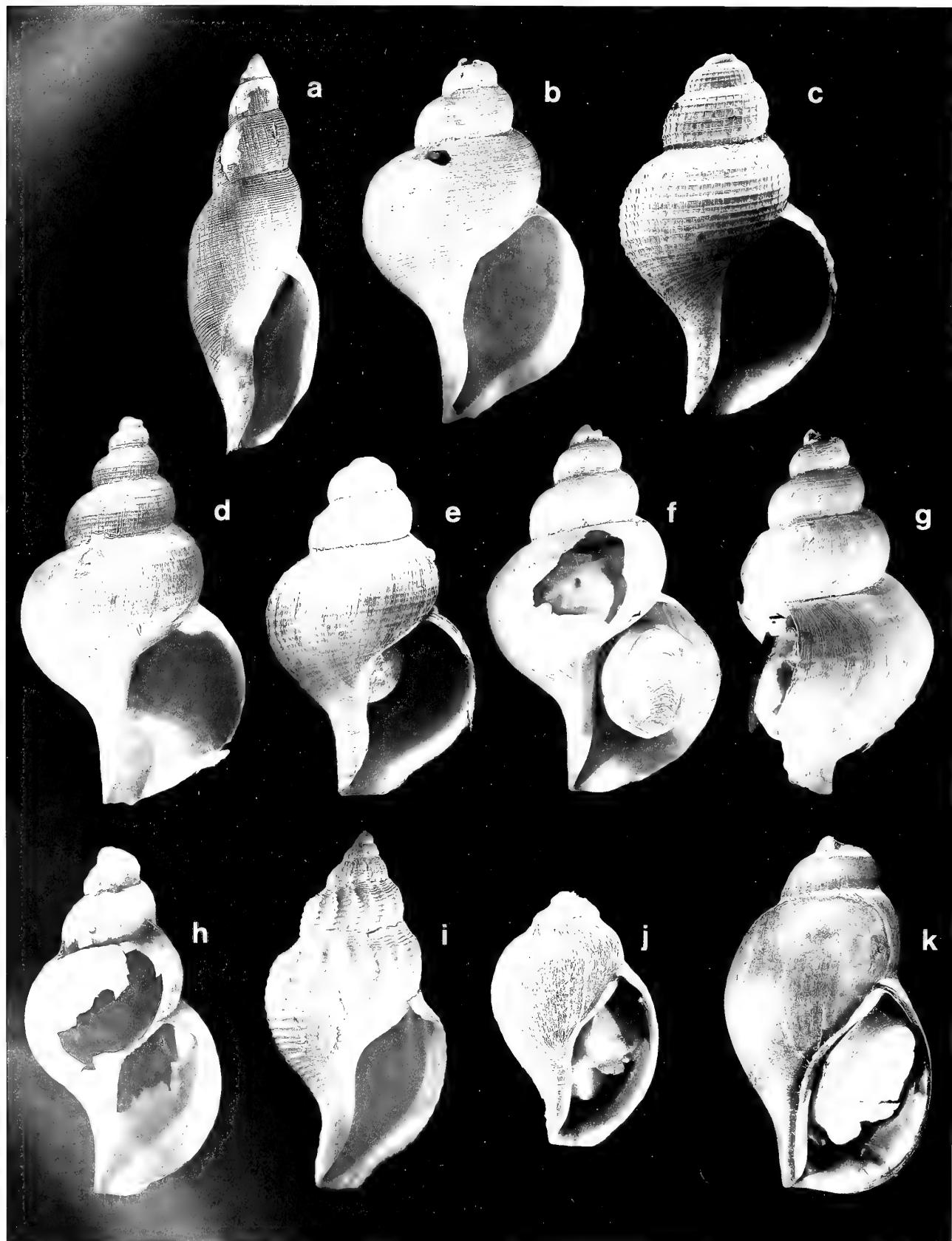
Material examined: Only known from the type series.

Distribution: Only known from the type locality.

Etymology: "peruvianus" after Peru.

Description: Shell (Figure 38h). Fusiform, extremely thin and fragile, with convex whorls and short siphonal canal. The protoconch is not known in any specimen, but the most apical whorl, of a diameter of 2.5–3 mm, has a uniform sculpture of 10–12 rounded spiral cords of equal size, and less than $\frac{1}{2}$ a teleoconch whorl seems to be missing. At a diameter of 5–6 mm the axial sculpture starts to become more conspicuous and consists of growth lines only. On later whorls the spiral sculpture usually is less conspicuous and the growth lines may dominate. The periostracum is brownish green, thin, and forms very low lamellae at the growth lines, slightly higher close to the suture. The aperture is a little shorter than half the height of the shell; the outer lip is not thickened; in profile it is distinctly sigmoid with a shallow sinus occupying the apical $\frac{2}{3}$; the siphonal canal is very short and open.

Dimensions. Maximum shell length (estimated) ca. 40 mm.



Radula (Figure 39c). The central tooth is low and has three cusps of equal size. The anterior and posterior margins are approximately parallel. The marginal plate has three strong cusps, the inner two slightly smaller.

Operculum (Figure 49d). Fan-shaped with nucleus corroded in all specimens. The shape is quite variable, from quite slender, as in the illustration, to about half the proportional length, i.e., ovate with lateral nucleus.

Remarks: This new species probably belongs to *Bayerius*, but it differs from the type species, *B. fragilissimus*, in being more stout with a shorter spire and more rapidly increasing diameter of the whorls. The sculpture of the present species is much weaker. The operculum of *B. fragilissimus* is not known, but Olsson (1971) figured the radula, which has tricuspidate laterals and a longer central plate than our species.

Bayerius arnoldi (Lus, 1981)

(Figures 38b–e, 39b, 49c)

Tacita arnoldi Lus, 1981:140, figs. 1–4.

Type material: Holotype (Figure 38b) in the Institute of Oceanology, Moscow.

Type locality: "Vityaz" sta. 3575, north-eastern Pacific, 37°56'N, 146°24'E, 5471 m.

Material examined: The holotype and: - "Vityaz" sta. 5624, 45°26'N, 154°12'W, 5200 m, 12 spms. *Aleutian Trench*: - ROPOS 344, 1 spm; - TVG 24, 3 spms; - TVGKG 40, 1 adult spm with hydroids (SMF 311999), 15 shs, 5 spms (all young); - TVG 48, 2 spms (SMF 311997); - TVGKG 49, 7 shs (SMF 311998); - TVG 63, 1 adult spm.

Distribution: Japan, Kuril, and Aleutian Trenches, 6135–4800 m depth.

Redescription: Shell (Figures 38b–e). Of medium size for the family, *Neptunea*-like, greyish, very fragile. The protoconch (Figures 38c, e) is not demarcated, but starts smooth, then adds spiral ridges and sharp incremental lines after ca. 0.75 whorl. The teleoconch has ca. 12–15 rounded spiral ridges of uniform strength on the most apical whorls; 20 sharp threads, weaker and stronger ones alternating on the penultimate whorl. On the body whorl the sculpture extends across the base with the same appearance. The whorls are strongly and evenly convex; the

suture deep. Our largest specimen has a little more than six whorls, but the apex is slightly corroded.

Dimensions. Largest good specimen 44.0 mm; maximum size 55 mm (estimated, spire broken).

Operculum (Figure 49c). Brownish, ovate, with about half a whorl and nucleus remaining.

Radula (Figure 39b). Normal for the genus.

Remarks: Our material was compared with the type in the Institute of Oceanology, Moscow. At 10 mm diameter, the holotype has seven stronger spiral cords which form small nodules at the intersections with the incremental lines; between these major cords there are three much smaller ones. In our specimens, at the same diameter, there are eight to nine major cords which hardly form any nodules, and there are only one or two spiral lines between them. Nevertheless, the shape and sculpture are close enough, and the specimens come from nearby localities so we believe them to be the same species.

Sahling (1997) assumed this species to be a predator on actinians which were common as epifauna on the clam *Calyptogena phaseoliformis* in the seeps.

The original description is in Russian and we have therefore redescribed *Bayerius arnoldi*.

Bayerius sp.

Material examined: Mid America Trench, Jalisco Block Seeps at 20°N: - NAUTIMATE PL 10, 1 sh.

Remarks: A single small shell (5 mm) differs from *B. arnoldi* in having taller and more slender whorls, but is too young for comparison with any of the more southern species of *Bayerius*, which are known only from large specimens with corroded apical whorls.

Buccinum Linnaeus, 1758

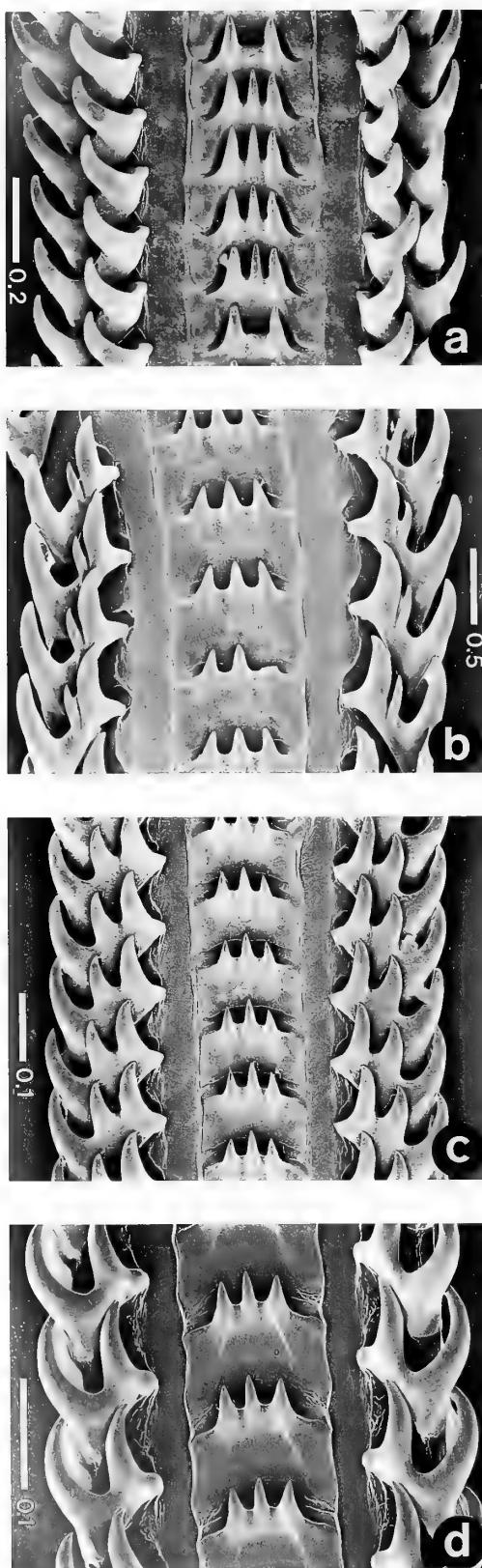
Buccinum Linnaeus, 1758:734.

Type species: *B. undatum* Linnaeus, 1758; by subsequent designation by Montfort (1810); northern Europe.

Remarks: The genus *Buccinum* is rich in species and taxonomic problems, due to a strong tendency to form local populations. The main distribution is northern and in shallow water, but scattered species occur down to about 2000 m depth. They are scavengers and predators.

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Figure 38. Neogastropod shells. a. *Tractolira sparta*, off Peru, 65 mm. b–e. *Bayerius arnoldi*. b. Holotype, 51 mm. c. Paratype, 13 mm. d. Aleutian Seeps, Edge site, 43 mm. e. Young specimen, Aleutian Seeps, Shumagin site, 12 mm. f, g. *Bayerius holosericeus*, holotype, 64 mm. h. *Bayerius peruvianus* Warén & Bouchet, sp. nov., holotype, 34 mm. i. *Eosipho canetae*, Bush Hill Seep, 52 mm. j, k. *Eosipho auzendei* Warén & Bouchet, sp. nov. j. Young specimen, 29 mm. k. Holotype, 62 mm.



Buccinum sp.

Records: JdF, Endeavour Segment: - ATV 50-1, High Rise vent field, 2 spms; - ROPOS #278, Main Field, 2 empty egg capsules, 2 capsules with 7–8 embryos each.

Remarks: The operculum is of normal *Buccinum* type, with concentric growth lines and the nucleus situated at the posterior $\frac{1}{6}$, slightly over to the left side. The head-foot is unpigmented and the eyes are deeply subcutaneous and lack pigment. Species of *Buccinum* usually live in more shallow water and have pigmented eyes. Also those that live in quite deep water (500–1000 m) have eyes, which indicates that these specimens are not occasional guests in the deep-sea fauna.

This is probably the species reported as *Buccinum viridum* Dall, 1890, in various places at JdF. The type locality of that species is situated 10° farther south, off Santa Barbara, California, but no details about this locality (Albatross 1887-8, station 2839, ca. 750 m depth) are known. Cold seeps are, however, common all along the California coast (K. L. Smith, personal communication), and it is possible that the Albatross hit such a place. This identification is supported by the fact that *B. viridum* was described as having unpigmented eyes, which is rare in the genus. According to J. McLean (unpublished), populations of *Buccinum viridum* are common along the California coast in deep water, but the taxonomy is uncertain.

Eosipho Thiele, 1929

Eosipho Thiele, 1929:307.

Type species: *Chrysodoma* (*Siphon*) *smithi* Schepman, 1911; by original designation; Celebes Sea, ca. 1200 m depth.

Remarks: The genus *Eosipho* contains about half a dozen bathyal species of uncertain relation. Two species are now known from hydrothermal vents, both of which have a thick periostracum and a mainly smooth shell, while those from normal environment have well developed axial and spiral sculpture and thin periostracum. It is uncertain whether the two vent species really belong to *Eosipho*, but hypertrophy of the periostracum, as is the case with these two species compared with others, is common among vent gastropods and can change the appearance considerably. Anyhow, the two vent species are quite similar to each other and presumably closely related. Undescribed species of *Eosipho* have regularly been recovered from sunken pieces of driftwood from deep dredgings in the tropical western Pacific (Bouchet, unpub-

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Figure 39. Buccinid radulae. a. *Eosipho auzendei* Warén & Bouchet, sp. nov., paratype. b. *Bayerius arnoldi*, Aleutian Seeps, Shumagin site. c. *B. peruvianus* Warén & Bouchet, sp. nov., paratype. d. *E. canetae*, Bush Hill Seep. Scale bars in mm.

lished), and Harasewych (1990) reported the related *Maria fusiformis* (Clench & Aguayo, 1941) from sunken wood.

Eosipho desbruyeresi Okutani & Ohta, 1993

Eosipho desbruyeresi Okutani & Ohta, 1993:217, figs. 1–5.

New records: *Lau Basin*: - BIOLAU PL04, 2 spms; - BIOLAU PL10, 1 juvenile spm.

Distribution: Lau and North Fiji Basins, in about 1750–2000 m depth.

Remarks: The top whorls, at a diameter of 7–8 mm and smaller, are axially ribbed, which is the normal sculpture of species of *Eosipho*.

Eosipho auzendei Warén & Bouchet, sp. nov.

(Figures 38j, k, 39a, 49a)

Type material: Holotype and 2 paratypes in MNHN.

Type locality: EPR at 17°S, Rehu site, 17°24.85'S, 113°12.15'W, 2578 m.

Material examined: The types and: *EPR at 17°S*: - NAUDUR PL19.1.2.b, site Rehu, 1 spm.

Etymology: Named after Jean-Marie Auzende, discoverer of many vent fields and expedition leader of NAUDUR.

Distribution: Only known from the type locality.

Description: *Shell* (Figures 38j, k). Large for the group, fusiform, smooth, brownish, with expanded peristome and very short canal. The uppermost whorls are lost by corrosion in all specimens. The most apical whorl in the young specimen has a diameter of about 6 mm and is sculptured with low, rather indistinct axial ribs which disappear on the subsequent whorls and are not present in any of the three adult specimens which have lost one more apical whorl. The shell is poorly calcified; $\frac{1}{4}$ whorl back from the outer lip its thickness is 0.5 mm of which the periostracum constitutes 0.2 mm. The periostracum has an outer layer of dense, soft axial lamellae, which probably wear off with time because they cover all the shell of the young specimen (Figure 38j), while they are restricted to the suture in adult specimens. Below this layer it is brown, smooth, and brittle. The suture is shallow, and rendered less conspicuous by the outer layer of the periostracum. The peristome is large, broad and expanded, especially in its lower part. The columella is covered by a well demarcated, thin, whitish calcareous layer. The outer lip is slightly thickened and reflected; its inside has a low rounded ridge paralleling the margin of the apical $\frac{2}{3}$ of its height.

Operculum (Figure 49a). It is brown, a little longer than half the aperture, triangular to ovate with distinct

growth lines, and its initial part is lost by abrasion. It is unusually soft and pliable and has a large semicircular, thinner attachment area bordered by a low ridge and a small callus below, at the left, inner part.

Radula (Figure 39a). The central plate is poorly demarcated, but has three strong cusps of equal size. The lateral tooth has two strong cusps, the inner one slightly smaller.

Soft parts. The foot is large and fleshy with demarcated propodium. The head is large with cephalic tentacles of a diameter of $\frac{1}{3}$ of that of the proboscis. The eyes are half the diameter of the tentacle and situated at the outer side of these. The specimen used for radular examination was a female, and no other specimen was dissected, hence the presence of a penis could not be verified. The gill is large and its anterior half paralleled by a dark brown, bipectinate osphradium.

Remarks: The stomach was full of partly digested, unidentifiable flesh, and the species is a scavenger and predator.

Eosipho auzendei resembles *E. desbruyeresi*, but has a higher aperture, $\frac{2}{3}$ of the height of the shell compared with half the height in *E. desbruyeresi*. *Eosipho desbruyeresi* also lacks the lamellar portion of the periostracum.

Eosipho canetae (Clench & Aguayo, 1944)

(Figures 38i, 39d, 49b)

Buccinum canetae Clench & Aguayo, 1944:64, fig. (not numbered).

“*Buccinum*” *canetae*: Warén & Bouchet, 1993:76, fig. 59 D.

New records: *Off Louisiana*: - Johnson Sealink dive 3129, 14 spms.

Distribution: From the Louisiana Slope to Surinam in 420–850 m depth.

Remarks: We transfer *Buccinum canetae* to *Eosipho*, based on similarities to the type species of *Eosipho* in shell, operculum, and radula. The animal lacks eyes. We figure the radula (Figure 39d) and operculum (Figure 49b), which agree well with other species of this genus (see Bouchet & Warén, 1986). The type species of *Eosipho*, *E. smithi*, differs in having no axial sculpture, but the shape of the aperture and the whorls, especially the slight constriction just below the suture make *B. canetae* fit better here than in any other of the deep water buccinid genera, and certainly much better than in *Buccinum* where it has been classified until now. *Eosipho canetae* is probably not an obligate member of the seep faunas since it was described from regular dredging, but it seems to be more common at the seeps.

Family VOLUTIDAE Rafinesque, 1815

Tractolira Dall, 1896*Tractolira* Dall, 1896:12.**Type species:** *T. sparta* Dall, 1896; by original designation; abyssal, off Central America.*Tractolira sparta* Dall, 1896

(Figure 38a)

Tractolira sparta Dall, 1896:13.*Tractolira sparta*: Dall, 1908b:299, pl. 2, fig. 7; Poppe & Goto, 1992:121, pl. 39, figs 7, 8 (holotype).**New records:** Off Peru, Paita area: Between 5°34' and 5°38'S, 81°54' and 81°35'W, 5300–3100 m, 1 spm.**Distribution:** Described from four localities between Acapulco, Mexico, to the Gulf of Panama, in 3043–4062 m, no further records known.**Remarks:** This single specimen (67 mm high) had been brought back by an expedition to the Peruvian seeps with no indication of precise locality, but the species is poorly known and this record represents a considerable range extension, so we have included it. Poppe & Goto (1992) summarized the present knowledge about the genus.

Family CONIDAE Fleming, 1822

Remarks: The classification of the Turridae was recently reconsidered by Taylor et al. (1993) who transferred the subfamily Daphnellinae which contains the species below, to the Conidae. Their classification, however, was challenged by Rosenberg (1998), who considered that “malacologists will be justified in retaining the traditional classification, until more robust evidence for transferring [Daphnellinae] to Conidae is produced.”

Conid type egg capsules are frequently found in vent environment, attached on rocks and shells. Two types were described by Gustafson et al. (1991), as “inflated triangular capsules” (from the Galapagos Rift) and “lenticular egg capsules” (from EPR at 21°N), but not assigned to genus, although the former type was convincingly assigned to the “Turridae.”

We have egg capsules of the former type from the EPR (13°N) and MAR (Snake Pit) (Figures 40b, c), both from localities where species of *Phymorhynchus* are common. Regrettably they were empty or contained eggs only, so we have not been able to examine larvae with a shell. However, even if they had contained veligers with a shell and ready to hatch, protoconch 1 should probably not be specific enough in its sculpture to allow closer identification than the family Conidae. Furthermore, since we do not know the detailed sculpture of the protoconch 1 of any of the vent turrids, we could not have identified it by comparison with identified specimens. It seems, however, likely that the “inflated triangular capsules” (Gustafsonet al., 1991) belong to *Phymorhynchus*, judging from the occurrence together with specimens of that genus, at three widely separate localities. Also the “lenticular egg capsules” have most likely been deposited by a conoid species as suggested by Gustafson et al. (1991), perhaps a different species of *Phymorhynchus*, judging from the large size.

We want to take this occasion to draw the attention to another type of egg capsules that we frequently have received, identified as “belonging to gastropods.” Turbellarians of the family Fecampidae (Rhabdocoela) produce capsules very similar to those of gastropods and of a similar size (Figures 40a, c). For further information about these, see Möller Christensen (1981).

We have noticed that the radular teeth of species of *Phymorhynchus* change shape and size with the size of the specimen (Figures 43b–d). The length of the teeth increases more slowly than the height of the shell and the shape of the teeth may change. This has previously not been recognized, but should be considered when the radula is used for identification or phylogenetic work.*Phymorhynchus* Dall, 1908*Pleurotomella* (*Phymorhynchus*) Dall, 1908b:258.**Type species:** *Pleurotomella* (*Phymorhynchus*) *castanea* Dall, 1908; by original designation; deep water east of Galapagos.**Remarks:** Dall (1908b) described several species of *Phymorhynchus* from 1500–4000 m depth from the tropical eastern Pacific. These, however, are all more slender than the species described below from the EPR.The species of *Phymorhynchus* from hydrothermal vents are all quite similar to each other, more so than to any of the species from non-vent environments that we have examined (Bouchet & Warén, 1980) or those described by Dall (1908b). The species from the ambient deep-sea have more developed axial ribs and the spiral cords are more distinctly differentiated in size and appearance by the fact that the more apical ones are stronger and separated by wider interspaces than the abapical ones. The genus can be recognized by the large rhynchodeum, large size, presence of mainly spiral sculpture, and total absence of subsutural (anal) sinus in the shell (except in very small specimens).Sysoev & Kantor (1995) described the anatomy of the head-foot of *P. moskalevi* and *P. wareni*. We figure a critical-point dried specimen of *P. ovatus* to show the huge funnel-shaped rhynchostome (Figure 40d), actually formed from the head and the area around the proboscis opening. The real proboscis is small and usually everted in the bottom of the funnel. The cephalic tentacles are small, cylindrical, and situated far apart on the head. None of the species we have examined have eyes. Almost all specimens have a penis at some stage of development,

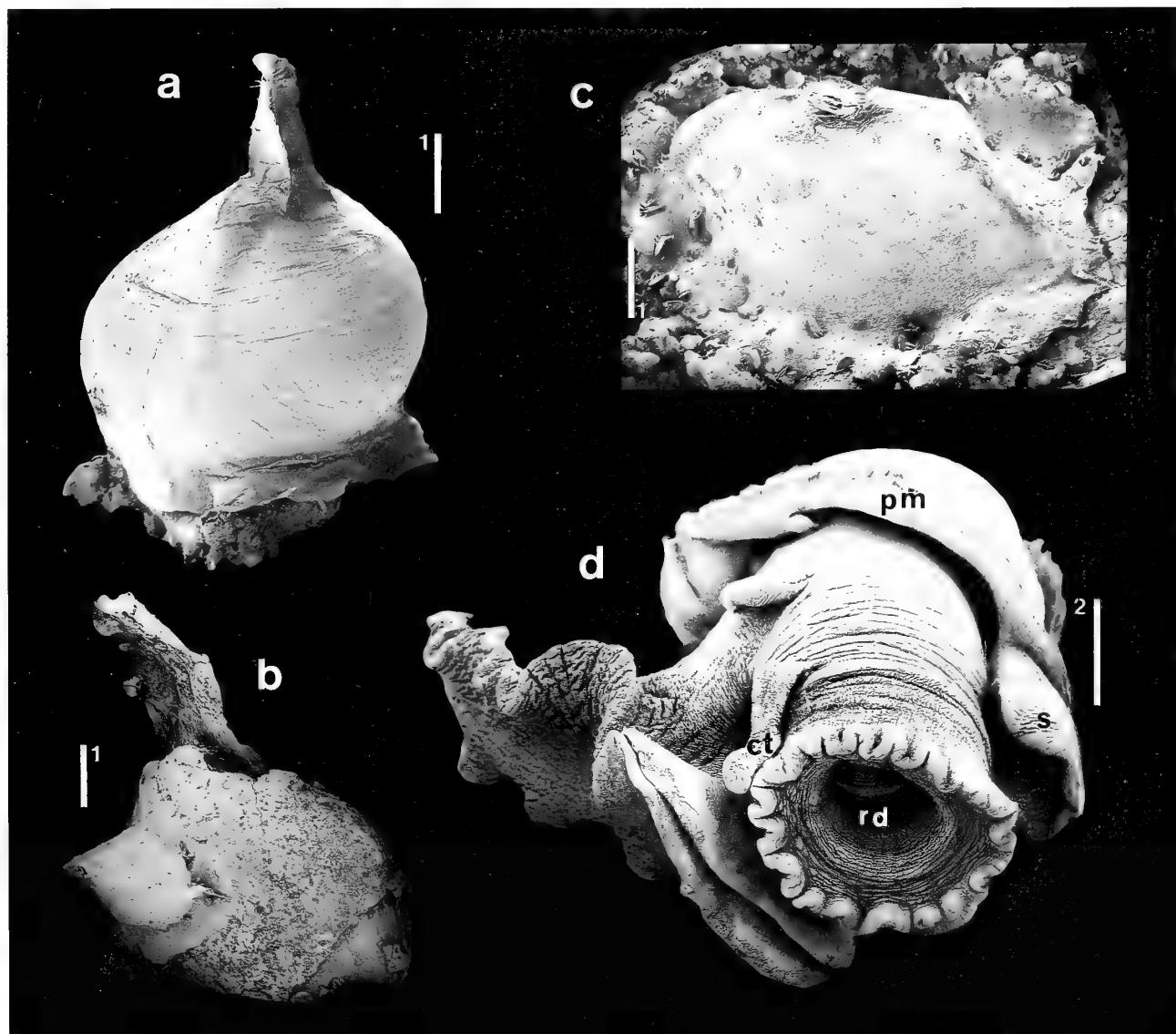


Figure 40. *a.* Turbellarian (Rhabdocoela) egg capsule, MAR, Lucky Strike, height 5.7 mm. *b, c.* *Phymorhynchus* sp., egg capsule, MAR, Lucky Strike. *b.* On turbellarian egg capsule. *c.* On a rock. *d.* *Phymorhynchus* sp., MAR, Lucky Strike. ct - cephalic tentacle; pm - pallial margin; rd - rhynchodaeum; s - siphon. Scale bars in mm.

from a small wart behind and below the right cephalic tentacle, to a large, flat structure with an apical papilla. This may be present in combination with a pallial oviduct, independently of sex and size of the specimen. It seems more to be a case of "imposex" than actual hermaphroditism, but this needs verification by histological examination of the gonad. (If this is a case of imposex, it does not seem likely that it is caused by tributyl tin, since these localities are as far from sources for those compounds as one can get. It seems more likely to be caused by effluents from the vents.) The right edge of the siphonal canal continues as a skin fold inside the pallial margin, where it turns abruptly to the right and forms a

drape hanging from the pallial roof, closing the space between the back of the snail and its pallial skirt, and directing the outflow of respiratory water to the right ¼ of the cavity. This curtain was noticed in all species listed below.

A specimen of *Phymorhynchus* sp. from the EPR had eaten *Neomphalus fretterae* (Warén & Bouchet, 1991), and two specimens of *P. ovatus* from the MAR had eaten *Bathyymodiolus*, two had remains of a worm-shaped animal (not a polychaete) in their esophagus. M. Segonzac (personal communication) has seen a specimen eating a fresh shrimp, *Rimicaris exoculata*, at the Snake Pit site, but did not know if the snail had caught it alive or found it dead.

No protoconchs have been available, except some brown remains in the smallest specimens (Figure 42a) which unambiguously show that the species have planktotrophic larval development. A single young specimen from MICROSMOKE PL 20, 2.6 mm high, had one complete whorl left of protoconch 2, maximum diameter 0.8 mm. Judging from this remaining whorl, it closely resembles the protoconch we (Bouchet & Warén, 1980, fig. 238) assumed to be *P. alberti*, but perhaps slightly lower, and a height of 0.7 mm above the teleoconch suture seems likely. In young specimens, up to 4–8 mm teleoconch height, the anal sinus is more conspicuous, and below 4–5 mm the spiral sculpture is quite weak.

Species of *Phymorhynchus* should probably make a suitable object for molecular study of vent species with planktotrophic development: they are common and easy to identify to genus, there are several species, they are often collected because of their large size, which also makes it possible to save enough material of each specimen for regular taxonomic work.

Four additional species of *Phymorhynchus*, not discussed below, have been described: *P. starmeri* Okutani & Ohta, 1993, and *P. hyifluxi* Beck, 1996, from the North Fiji Basin, *P. wareni* Sysoev & Kantor, 1995, from the Edison Seamount, and *P. buccinoides* Okutani, Fujikura & Sasaki, 1993 from seeps at the Hatsushima site in Sagami Bay.

Phymorhynchus ovatus Warén & Bouchet, sp. nov.

(Figures 41e–g, 42a, b, 43b–d)

Type material: Holotype and 6 paratypes in MNHN.

Type locality: MAR at Logatchev site, MICROSMOKE PL 20, Irina site, 14°45.10'N, 44°48.60'W, 3005 m.

Material examined: The types and: MAR, *Lucky Strike*: - DIVA 2: 02, 1 spm; - ALVIN dive 2607, 2 spms. *Snake Pit*: - HYDROSNAKE PL 10 (Les Ruches), 11 spms; - GRAVINAUT PL 01-2 (Les Ruches), 1 spm; - ALVIN dive 2615 (Elan), 1 spm, crushed; - ALVIN dive 2619 (Elan/Ruches), 3 spms, 1 young, 8 egg capsules on rocks and on a turbellarian egg capsule; - ALVIN dive 2620 (Elan/Ruches), 4 spms; - ALVIN dive 2621 (Elan), 2 spms, 1 young; in trap, 13 spms; - MICROSMOKE PL 08, Ruches site, in trap, 10 spms; - MICROSMOKE PL 14, 1 spm; - MICROSMOKE PL 16, 3 spms; - MICROSMOKE PL 17, Elan, 5 spms. MAR 14°45'N: - MICROSMOKE PL 21 (Irina), 1 spm.

Distribution: MAR, from *Lucky Strike* to Logatchev site, in 1600–3500 m depth.

Etymology: From “*ovatus*” (Latin), shaped like an egg.

Description: *Shell* (Figures 41e–g). Large, colorless,

fragile, buccinoid, with uniform spiral sculpture, brown periostracum, and rounded aperture. The apex and protoconch are not known in detail, but the shells in Figures 42a, b probably belong here. The teleoconch has had about 4.5 whorls (estimated; \pm 0.5 whorls) of rapidly increasing diameter. The sculpture consists of spiral cords, 18 on the last whorl close to the outer lip, four to five on the penultimate whorl, and four on the whorl before. More apically no trace remains of them because of corrosion. The cords are evenly rounded, much broader than the interstices, covered by 15–20 fine, undulating lines, and increase in size toward the apical part of the whorls. The incremental sculpture is visible mainly on the last half whorl of the shell and consists of numerous irregular, weak lines and scattered stronger scars. The outermost layer of the shell and the brownish periostracum are usually worn off or corroded on the whole shell, except sometimes in the interspaces between the ribs and close to the lip. The whorls are evenly convex and the suture very shallow. The aperture is high and elongate, its outer lip not thickened, in profile unusually straight and without a trace of a labial sinus. The relation between the total height of the shell and the maximum diameter of the peristome varies individually between 1.34 to 1.39 (15 specimens between 13 and 67 mm shell height). The siphonal canal is very short, and the lower part of the outer lip projects below the end of the columella.

Dimensions. Height of holotype 49 mm, largest specimen 67 mm.

Soft parts. As in the genus, operculum absent. The penis is flat, apically truncated with a smooth flat surface surrounding a papilla. The anterior edge is finely wrinkled, the posterior, apical third has a folded glandular area.

Radula (Figures 43b–d). Length of teeth 270 μ m in a specimen of 55 mm shell height, 220 μ m at 39 mm, 130 μ m at 10 mm.

Remarks: Two specimens from ALVIN dive 2620 had disgorged their partly digested prey, which still was firmly anchored in the rhynchostome. It was identified, from the gills, paired pedal retractors, and paired gonads, as remains of mytilids. Two specimens from ALVIN dive 2621 had vomited wormlike animals, and one had thrown up a mass of flesh.

Phymorhynchus ovatus is not always easy to distinguish from *P. moskalevi* but the ovoid shape and the evenly curved profile of the whorls help. At a size of 13–30 mm, *P. ovatus* has four rather distinct furrows at the end of the penultimate whorl; when adult it has five (rarely six) of them. *P. moskalevi* has indistinctly shouldered whorls and a relation between maximum diameter of peristome and shell height varying between 1.47 and 1.60 (10 specimens in the size range 10–40 mm). They have a subsutural zone with indistinct spiral furrows and below these six to seven spiral furrows at the end of the pen-

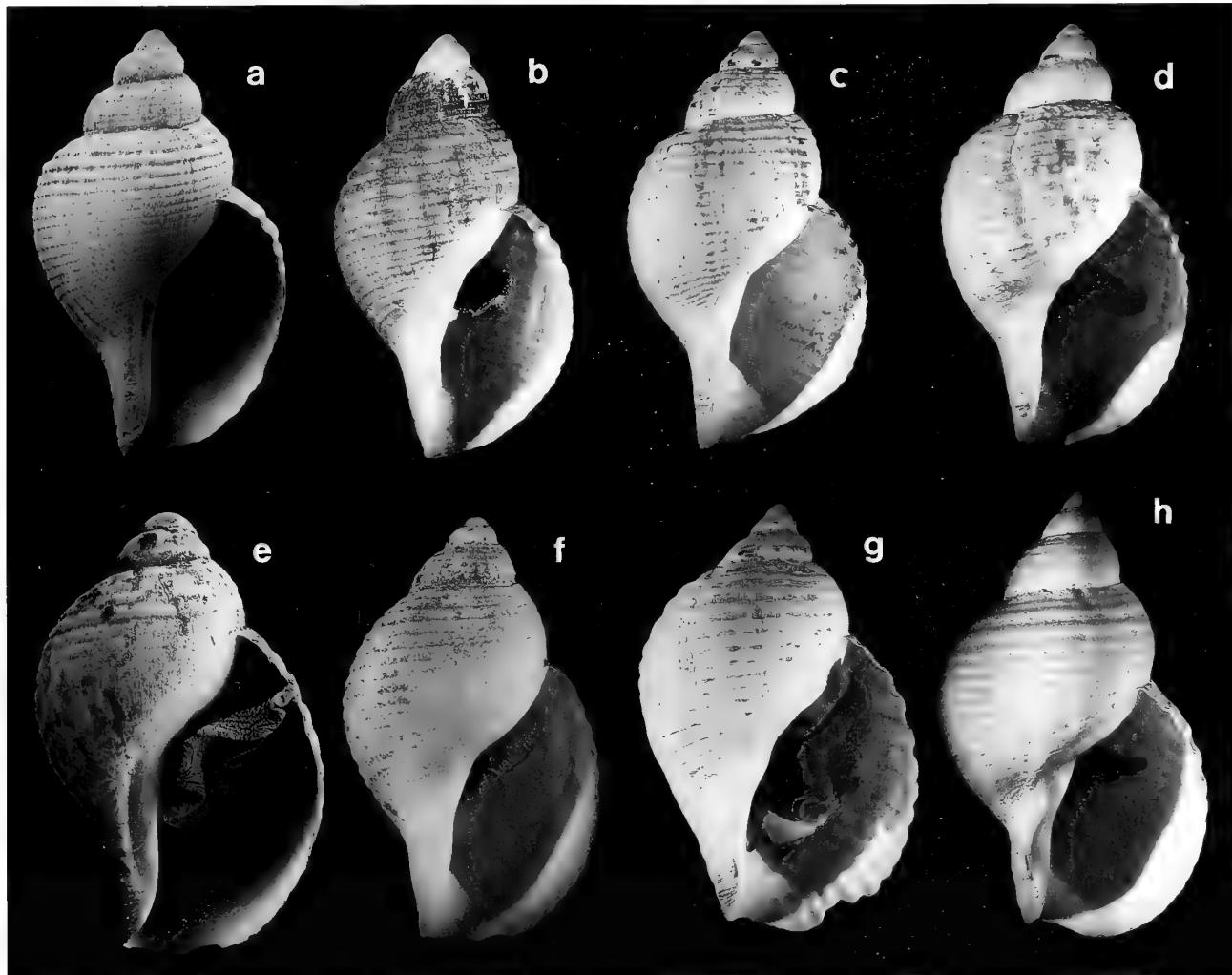


Figure 41. *Phymorhynchus* spp. a–d. *P. moskalevi*. a. Young specimen, MAR, Snake Pit, 10.3 mm. b. Subadult, MAR, Snake Pit, 28.4 mm. c. Adult, MAR, TAG field, 39 mm. d. Adult, MAR, Snake Pit, 38.5 mm. e–g. *P. ovatus* Warén & Bouchet, sp. nov. e. Young specimen, MAR, Snake Pit, 13.5 mm. f. Adult specimen, MAR, Lucky Strike, 38.5 mm. g. Large specimen, MAR, Logatchev site, 49 mm. h. *P. major* Warén & Bouchet, sp. nov., holotype, EPR, 13°N, 71.5 mm.

ultimate whorl. The radular teeth have a tendency to be slightly thicker in *P. ovatus*, but this was not perfectly clear from examination of four adult radulae of each.

Phymorhynchus moskalevi Sysoev & Kantor, 1995

(Figures 41a–d, 43e, f)

Phymorhynchus moskalevi Sysoev & Kantor, 1995:22, figs. 1H–I, 4, 5D–F.

New records: TAG: - Kremlin site, 2 spms (Tyler). Snake Pit: - MICROSMOKE PL 08 in a trap at the Ruches site, 75 spms; - MICROSMOKE PL 14 (Elan), 1 spm.

Distribution: MAR between 26 and 23°N, in 3400–3700 m depth.

Remarks: For differences from *P. ovatus*, see under that species.

Phymorhynchus carinatus Warén & Bouchet, sp. nov.

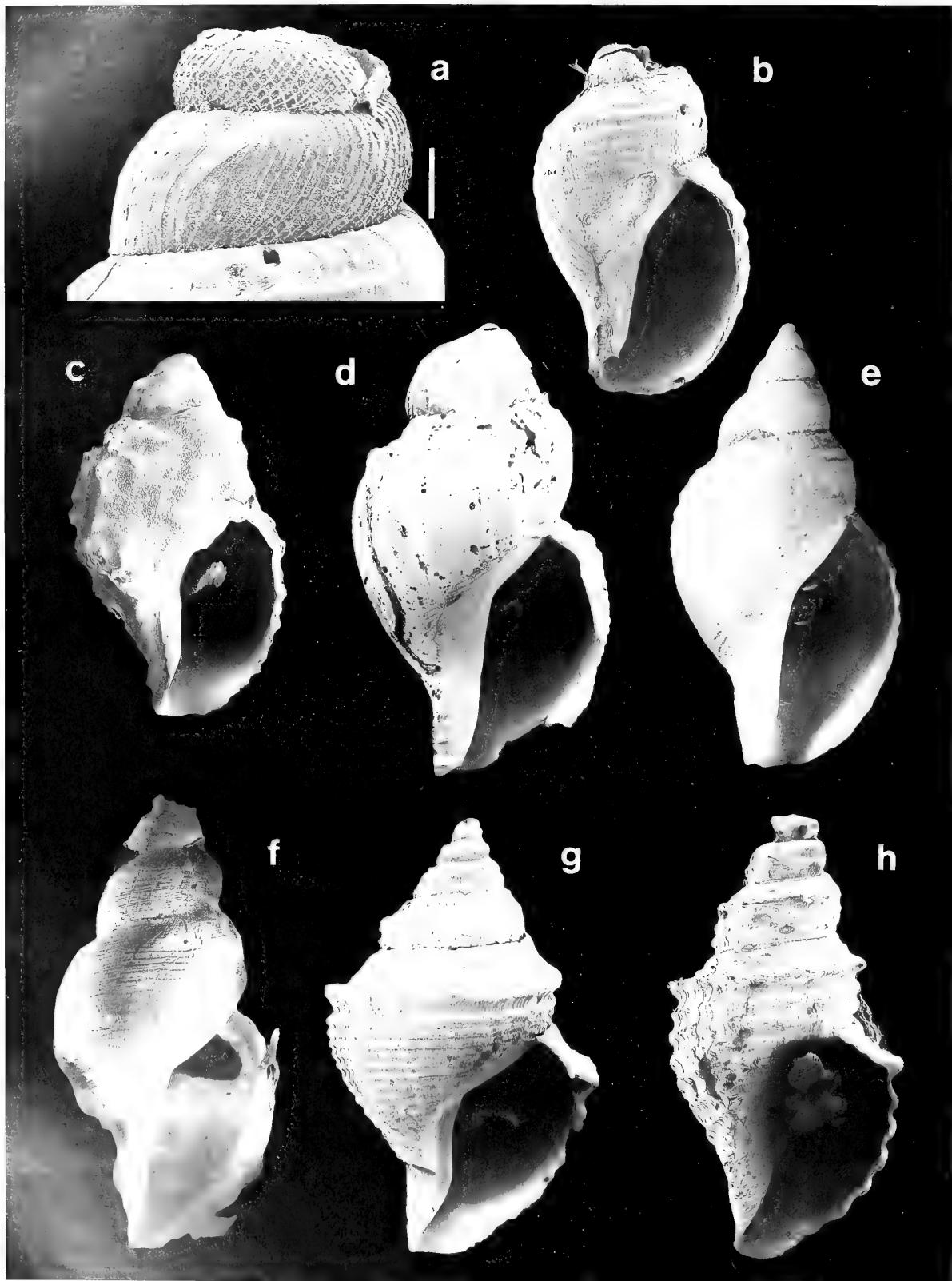
(Figures 42g, h, 43g–i)

Phymorhynchus sp. 2: Warén & Bouchet, 1993:79.

Type material: Holotype and 5 paratypes in MNHN.

Type locality: MAR at the Logatchev site: MICROSMOKE PL 20, 14°45'N, 44°59'W, 3040 m, Irina.

Material examined: The types and the two specimens from Snake Pit, recorded by Warén & Bouchet (1993).



Distribution: Snake Pit and Logatchev site, ca. 3000–3500 m depth.

Etymology: “*carinatus*,” Latin, meaning keeled.

Description: Shell (*Figures 42g, h*). Small for the genus, colorless, fragile, fusiform, with uniform spiral sculpture, a strong peripheral keel, and rounded aperture. The apex and protoconch are not known in detail, all specimens are badly corroded apically, and only traces of an apparently normal, brownish yellow planktotrophic type protoconch can be seen in the holotype (*Figure 42g*). The teleoconch has had about five whorls (± 0.5 whorls) of slowly increasing diameter. The sculpture consists of spiral cords, five above the strong peripheral keel on the last whorl, 18 below the keel; two or three above and one or two below at the beginning of the penultimate whorl. More apically no trace remains of them. The cords are evenly rounded, much broader than the interstices and twice as wide and high below the keel as above. The incremental sculpture is indistinct and irregular. The whorls are not very convex and the suture very shallow. The aperture is high and slender, with a distinct internal, V-shaped furrow corresponding to the peripheral keel, its outer lip is not thickened, unusually straight and without a trace of a labial sinus. The siphonal canal is very short, and the lower part of the outer lip projects below the canal.

Dimensions. Height of holotype 10.9 mm, largest specimen 15 mm.

Soft parts. As in the genus, operculum absent. A penis was not present in any of the two specimens we examined for this. The snout is inconspicuous in specimens of 8–11 mm shell height, normally developed at 14–15 mm.

Radula (*Figures 43g–i*). Length of teeth 75 μm in a specimen of 5.6 mm, 90–100 μm in the holotype, and 140 μm in a large specimen of 15 mm.

Remarks: As shown by Figures 42g–h, *P. carinatus* is quite variable in shell shape, but these two specimens represent the extremes. We have selected a subadult specimen as holotype (*Figure 42g*), because this specimen has much better preserved sculpture than adult(?) ones. One of the specimens from Logatchev site had thrown up some half digested prey, which seems to be the pedal retractor muscles of a *Bathymodiolus*.

Phymorhynchus major, sp. nov.

(*Figures 41h, 43a*)

Phymorhynchus sp.: Warén & Bouchet, 1989:95, figs. 115–116.

Type material: Holotype (dry), one complete and one crushed paratype in alcohol (MNHN).

Type locality: EPR at 09°50'N, HERO 91 PL 09, 09°50.20'N, 104°17.40'W, 2505 m, Worm Barbecue site.

Material examined: The types and specimens reported by Warén & Bouchet (1989).

Distribution: Known from the EPR at 13° and 09°50'N, at a depth of ca. 2500–2600 m. See remarks.

Etymology: “*major*” Latin, from its large size.

Description: Shell (*Figure 41h*). Large, colorless, fragile, *Buccinum*-like in shape, with uniform spiral sculpture and rounded aperture. The apex and protoconch are not known, all specimens are badly corroded apically. The teleoconch has had about six whorls (estimated; ± 0.5 whorls) of rapidly increasing diameter. The sculpture consists of spiral cords, 25 on the last whorl close to the outer lip, nine on the penultimate whorl, and eight on the whorl before. More apically no trace remains of them. The cords are evenly rounded, much broader than the interstices and increase in size toward the apical part of the whorls. There is no incremental sculpture visible except a few lines close to the outer lip, but the outermost layer of the shell and the thin brownish periostracum have been worn off or corroded on the whole shell, except in the interspaces between the ribs, close to the lip. The whorls are not very convex and the suture very shallow. The aperture is short and rounded, its outer lip not thickened, unusually straight and without a trace of a labial sinus. The siphonal canal is very short, and the lower part of the outer lip projects below the canal.

Dimensions. Height of holotype (largest specimen) 72 mm.

Soft parts. As in the genus, operculum absent. The penis is flat, apically truncate with a smooth flat surface surrounding a papilla. The anterior edge is finely wrinkled, the posterior, apical third has a folded glandular area.

Radula (*Figure 43a*). Length of teeth 330 μm (in a 55 mm male).

Remarks: Species of *Phymorhynchus* seem to be regularly occurring at the EPR sites, judging from video recordings, but have not been collected very frequently. This may be because they are too large and rare to be included in sediment and vestimentiferan samples, and because their shells are fragile and break when collected with the mechanical arms of the submersibles.

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Figure 42. Conidae, shells. a, b. *Phymorhynchus ovatus* Warén & Bouchet, sp. nov., MAR, Logatchev site, scale bar 0.2 mm, height 3.5 mm. c. *Gymnobela* sp. B, MAR, Snake Pit, 13.3 mm. d. *Gymnobela* sp. A, EPR, 13°N, 12 mm. e. *P. aff. alberti*, End of Barbados Prism, 26.3 mm. f. *Bathybela papyracea* Warén & Bouchet, sp. nov., off Jalisco, height 95 mm. g, h. *P. carinatus* Warén & Bouchet, sp. nov., MAR, Logatchev site. g. 10.9 mm. h. Young specimen, 5.4 mm.



Phymorhynchus aff. *alberti* (Dautzenberg & Fischer, 1906)
 (Figure 42e)

Phymorhynchus alberti Dautzenberg & Fischer, 1906:16, pl. 1 figs. 8–10.

Phymorhynchus alberti: Bouchet & Warén, 1980:27, figs. 40, 72–73, 239.

New records: *Barbados*: - MANON PL 06 (north of Barbados), 3 broken spms; - DIAPISUB 10-4 (Oreonoque), 1 spm.

Distribution: Known from the north-eastern Atlantic between 16°N and 47°N, in ca. 1850–4800 m depth.

Remarks: One male from MANON had a simple, fingerlike, penis, tapering into a small apical papilla. A second specimen had a very small fingerlike process only. The identification of our specimens is doubtful. The MANON specimens are badly corroded, slightly broken, and unusually tall-spined; that one from DIAPISUB is not adult. It is therefore uncertain if these records are misidentifications or a westward extension of the range of *P. alberti*. The records are, however, of interest to show the presence of the genus also in seeps in the Atlantic Ocean.

Gymnobela Verrill, 1884

Gymnobela Verrill, 1884:157.

Type species: *G. engonia* Verrill, 1884; by subsequent designation by Cossmann (1896:63); bathyal North Atlantic.

Remarks: The genus has never been thoroughly revised and our use of this name is more a consequence of recent usage of the name for a number of Atlantic and West Pacific deep-sea species (e.g., Bouchet & Warén 1980, Sysoev, 1997), than based on a systematic selection among the ca. 900 generic names available for the Conoidea. The three species *G. extensa* (Dall, 1881), *G. sagamiana* (Okutani & Fujikura, 1992) (*comb. nov.*), and *G. sp. A* are quite similar in shell characters and have the same type of radula. We therefore believe this to be a group of species adapted to vent environment. They differ from *Phymorhynchus* in having very small snout and comparatively large cephalic tentacles. All three species lack eyes. Possibly also *Gymnobela* sp. B, from the MAR, belongs here, but it is in too poor condition for more than a guess.

Gymnobela extensa (Dall, 1881)

Gymnobela extensa: Warén & Bouchet, 1993:78, fig. 59A–C.

New records: Off Louisiana:-Johnson Sealink dive 3129, 17 spms.

Distribution: From the Yucatan Channel to off Louisiana in 512–1463 m depth.

Gymnobela sp. A
 (Figure 42d)

Material examined: EPR at 13°N: - HERO 91 PL 11, 1 spm; - HERO PL 12, 8 spms; - HERO PL 21, 1 spm; - HERO 92 dive 2523, 8 spms.

Distribution: Only known from the EPR at 13°N.

Remarks: The specimens are too corroded to be described, but are probably conspecific.

Gymnobela sp. B
 (Figure 42c)

Material examined: MAR, Snake Pit: - MICROSMOKE PL 07 (Elan), 1 badly corroded spm.

Remarks: The specimen above is too corroded for meaningful attempts of identification; it is included more as an example of how badly many specimens (and often all specimens of certain species) get corroded in these environments.

Bathybela Kobelt, 1905

Bathybela Kobelt, 1905:275.

Type species: *Thesbia nudator* Locard, 1897; by subsequent designation by Dall (1918b); abyssal, North Atlantic.

Remarks: The Atlantic type species, *Bathybela nudator* resembles *B. papyracea*, but the new species is larger, much more fragile, has a proportionally lower aperture, fewer whorls, and weaker axial sculpture. The general shape resembles some of the non-vent species described in *Phymorhynchus* from the East Pacific, but they have a coarser sculpture and no trace of color pattern on the columella. As far as known, this is the largest West American turrid.

←

Figure 43. Turrid radular teeth. a. *Phymorhynchus major* Warén & Bouchet, sp. nov., EPR, 13°N, specimen 55 mm high. b–d. *P. ovatus* Warén & Bouchet, sp. nov. b. Young specimen, 10 mm, MAR, Snake Pit. c. Subadult specimen, 38 mm, MAR, Lucky Strike. d. Large specimen, 55 mm, MAR, Lucky Strike. e, f. *P. moskalevi*. e. Young specimen, 12 mm, MAR, Lucky Strike. f. Adult, 38 mm, MAR, TAG field. g–i. *P. carinatus* Warén & Bouchet, sp. nov. g. Young specimen, 5.6 mm, MAR, Snake Pit. h. Holotype. i. Large specimen, 15 mm, paratype. j. *Gymnobela* sp. A, EPR, 13°N. Scale bars in µm.

Bathybela papyracea Warén & Bouchet, sp. nov.
(Figure 42f)

Type material: Holotype in MNHN (in alcohol).

Type locality: Mid America Trench. Jalisco Block Seeps at 20°N: - NAUTIMATE PL 18, 20°05'N, 106°18'W, 3662 m.

Material examined: The holotype.

Distribution: Only known from the type locality.

Etymology: "papyracea" refers to the thin shell.

Description: Shell (Figure 42f). Tall, slender, fusiform, fragile, finely spirally striated, slightly shiny and pale beige in color. The first few whorls are lost by corrosion; the diameter of the most apical, partially lost one is 10.5 mm. 3.5 evenly convex teleoconch whorls of rapidly increasing diameter remain. The subsutural zone occupies slightly more than $\frac{1}{3}$ of the height of the whorls. This zone is demarcated only by the incremental lines being concave, instead of convex. The zone is sculptured by about a dozen raised spiral lines of variable strength but weaker than on the adjacent part of the whorl. Below the zone the whorls carry 10 additional, raised ribs, stronger toward the abapical suture, alternating with three to five much smaller ones in each interspace. The body whorl has 20 additional, more basal spiral cords. The axial sculpture consists only of incremental lines, more distinct in the apical part of the subsutural zone, almost disappearing below the zone. The aperture is high, the outer lip almost semicircular, thin, and fragile. The columella and parietal wall are covered by a thin glaze, following the shape of the underlying spiral ribs. The central part of the columella is darker brown than the rest of the shell, a color pattern also visible at the columella of the broken, most apical whorl.

Dimensions. Height of the holotype 98 mm.

Remarks: The shell is very fragile and it seems impossible to extract the soft parts without breaking the shell. Also drying the specimen in order to detach the columellar muscle was judged dangerous, since it probably should have cracked the shell by the contraction of the soft parts. We therefore have no information about the soft parts, except that there is no operculum.

The classification in the genus *Bathybela* is based on similarity in shell characters, and direct comparison with the type species.

The shell was carrying several specimens of a sea-anemone.

Subclass HETEROBRANCHIA

Family HYALOGYRINIDAE Warén & Bouchet, 1993

Remarks: Several species of this group live in the vents and seeps of the northeastern Pacific, from the Aleutian

seeps to those in the Galapagos Rift vents. They have been found in sediment samples and on rocks. The gut is filled with sediment.

The systematic position of the Hyalogyrinidae is uncertain; the affinity to some of the "lower heterobranchs" (*sensu* Ponder, 1991) is supported by the heterostrophic protoconch, the sculpture of its initial whorl and the very unusual structure of the jaw, but is seemingly contradicted by the rhipidoglossate radular type (not bilobed at the initial part!), which is shared by *Hyalogyrina*, *Hyalogryra*, and *Xenoskeanea* among the heterobranchs (See Warén et al., 1993).

Hyalogyrina Marshall, 1988

Hyalogyrina Marshall, 1988:982.

Type species: *H. expansa* Marshall, 1988; by original designation; on sunken, bathyal driftwood off New Zealand.

Remarks: In addition to the species discussed here, a few specimens were found at the Oregon seeps (TVG 18, shells in SMF), but were too poor to allow identification. The generic position was confirmed by examination of radula and jaw.

Hyalogyrina umbellifera Warén & Bouchet, sp. nov.

Figures 37e, g; 44h-j; 45a-d; 47d; 48a, b; 49i)

Type material: Holotype SMF 311986 and 125 paratypes, SMF 311987, 125 paratypes in MNHN.

Type locality: Aleutian Trench, Shumagin site, TVGKG 40, 54°18.17'N, 157°11.82'W, 4808 m.

Material examined: The type material and: Aleutian Trench: - TVGKG 49, 19 shs and spms (SMF 311988).

Distribution: Only known from the material above, Aleutian Trench, Shumagin site, in 4800 m.

Etymology: "umbellifera," Latin, the one who carries an umbrella, referring to the set of large flat tentacles on top of the head.

Description: Shell (Figures 44h-j). Large for the group, tall-spired, rather sturdy, smooth, greyish white with a very thin, slightly iridescent periostracum. The protoconch (Figures 37e, g) consists of about 0.8 whorls, diameter 280 μm , with a very small initial part sculptured by small, crowded pits, diameter 4–5 μm , to some extent spirally arranged and fused. Where this sculpture ends, the diameter starts to increase rapidly and the shell becomes perfectly smooth. The peristome of the protoconch is slightly constricted and its width is three times the width of the whorl where the sculpture stops. The teleoconch consists of about 3.5 almost perfectly smooth whorls; the precise number of an adult specimen cannot

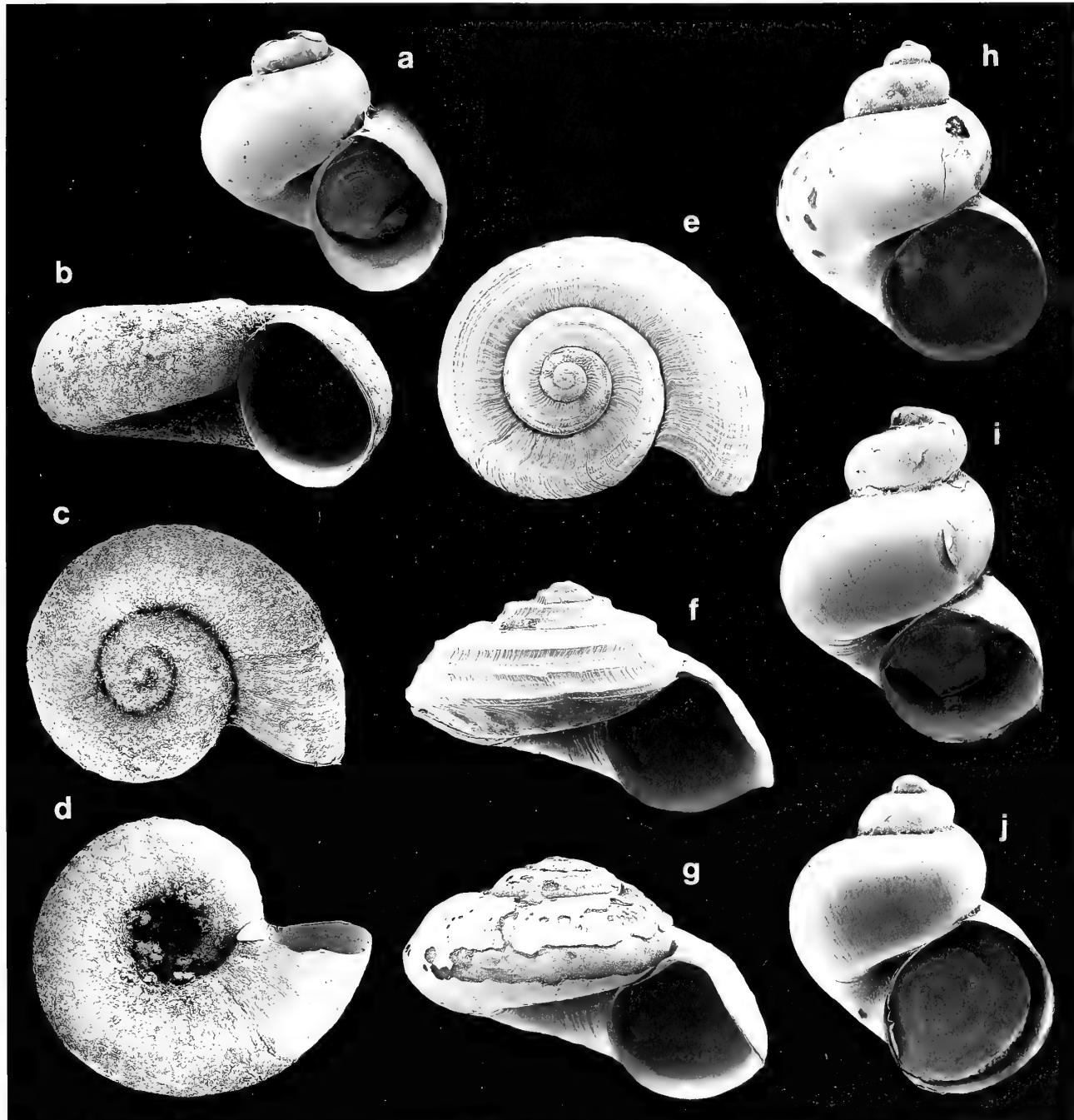


Figure 44. Heterobranchia, shells. *a*. *Hyalogyrina globularis* Warén & Bouchet, sp. nov., holotype, height 2.05 mm. *b–d*. *Xylodiscula analoga* Warén & Bouchet, sp. nov., holotype, diameter 1.7 mm. *e–g*. *Lurifax vitreus* Warén & Bouchet, gen. & sp. nov., MAR, Menez Gwen. *e*. Diameter 2.37 mm. *f*. Diameter 2.04 mm. *g*. Diameter 2.48 mm. *h–j*. *H. umbellifera* Warén & Bouchet, sp. nov., paratypes, height 3.2 mm, 3.2 mm and young specimen, 1.86 mm (*j*).

be given because all half-grown and larger specimens have lost the apex by corrosion. The suture is deep and the whorls not very firmly adjoining the preceding one. The entrance to the umbilicus is quite oblique and its width in a basal view corresponds to $\frac{1}{20}$ of diameter of

the shell. The peristome is prosocline, more tangential than radial, not thickened, and not indented by the preceding whorl. The cross section of the whorls is almost circular, except for the part of the inner lip which borders the umbilicus; this is almost straight.

Dimensions. Maximum height ca. 3.4 mm.

Soft parts (Figures 45a-d). The foot is very large, broad, and flat, posteriorly rounded with a shallow notch, anteriorly shallowly bilobed, and lacking a demarcated propodium. An epipodial ridge starts at the anterior part of the operculum, continues forward and reaches the base of the cephalic tentacles. The cephalic tentacles are about as long as the snout in preserved specimens, and are ciliated along the edges. At the central side each has large skinfolds, attached along its proximal half and to the basal part of the snout. The right tentacle has two of these, an upper one which is flat, distally broader, attached more basally and has four small digits and a lower one, which is partly covered by the upper one, is attached along the basal, central half of the tentacle. The left cephalic tentacle has a basally attached, fan-shaped fold, which also is fused to the basal part of the more ventral fold from the right tentacle. Together these folds form a complete cover over most of the snout. The snout is almost cylindrical, strongly transversally folded, slightly expanded distally, and has an apical-ventral mouth. The slender buccal mass is longer than the snout, has salivary glands opening to the buccal cavity, jaws composed of apically denticulate rodlets, and a short "rhipidoglossate" radula with simple, rounded end of the radular sac. The pallial cavity is rather deep, half a whorl; and the bipectinate gill is situated in the middle of its depth. The pallial margin is distinctly thickened and has a densely ciliated tentacle at its right corner. The inner, posterior half of the cavity is filled by invaginated pallial roof, with a loop of the large intestine. The stomach and intestine contain grey sediment; in the intestine the fecal rod is partly split by a deep longitudinal furrow.

Operculum (Figure 49i). Round, multispiral, with distinct growth lines, brownish flesh colored. The width of the last whorl, at the growth zone, corresponds to $\frac{1}{5}$ of the diameter.

Radula (Figures 47d, 48a, b). Ca. 15 - 1 - 1 - 1 - ca 15, short, 3-3.5 times as long as broad, rhipidoglossate, with marginal teeth folded across laterals and centrals. The central tooth is low and broad with projecting lateral supports, a triangular, finely serrated apical plate and distinct "wings" behind the lateral support. The lateral tooth is low and broad, its central half forms a triangular plate with finely serrated central side and a more coarsely denticulate outer side with irregularly scattered larger denticles. Its outer half is simple, and lacks dentation. The first marginal is flattened, with a dorsal, regular comb of small denticles, an apical finely serrated truncation, and an equally fine ventral serration. The basal $\frac{2}{3}$ of its length

lacks serration. The second marginal is longer, more slender, and both sides of the apical half are denticulate. Toward the side, the teeth become slightly shorter, more slender, and oar-shaped.

Jaw. Bipartite and consists of numerous rods in a ti-lelike arrangement, each equipped with three to five denticles at their free (inner) end.

Remarks: *Hyalogyrina umbellifera* has the tallest shell of the species of this genus, and is also characterized by the development of the cephalic tentacles. The protoconch and radula seem to be identical in all species.

Hyalogyrina globularis Warén & Bouchet, sp. nov.

(Figures 37f, 44a, 46a, 47e, f)

Type material: Holotype and one paratype (FMNH 279656 and 280923).

Type locality: JdF, Endeavour Segment, Clam Bed Vent Field, ROPOS HYS 351, 47°57.780'N, 129°05.493'W, 2200-2250 m, 3 spms (1 used for critical-point drying and radular preparation).

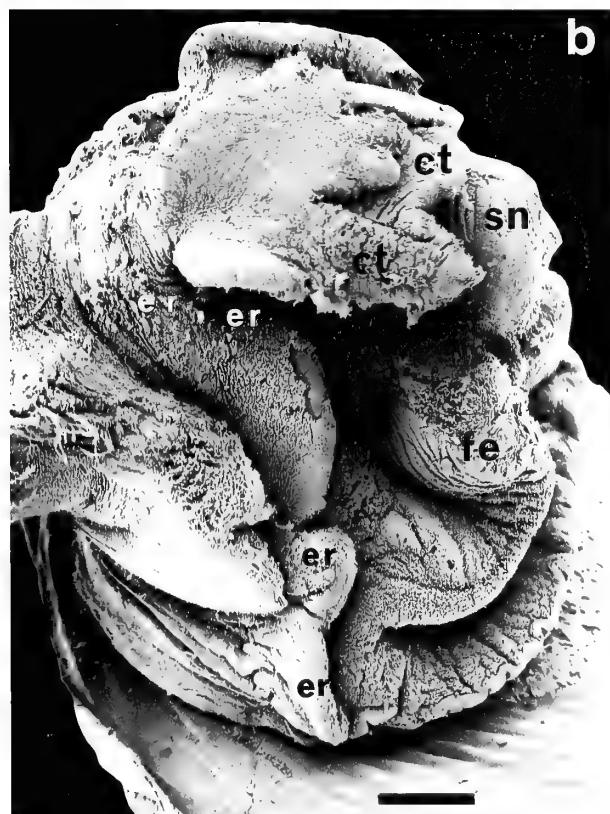
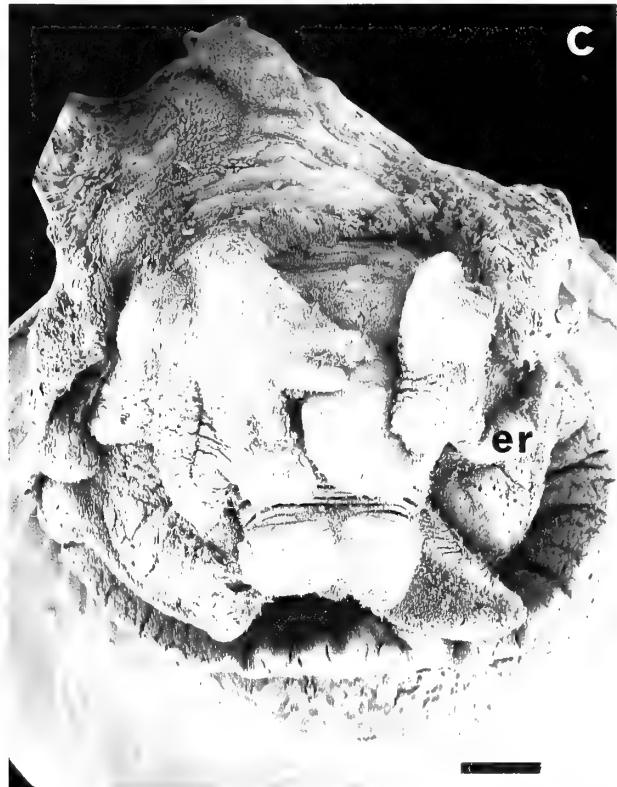
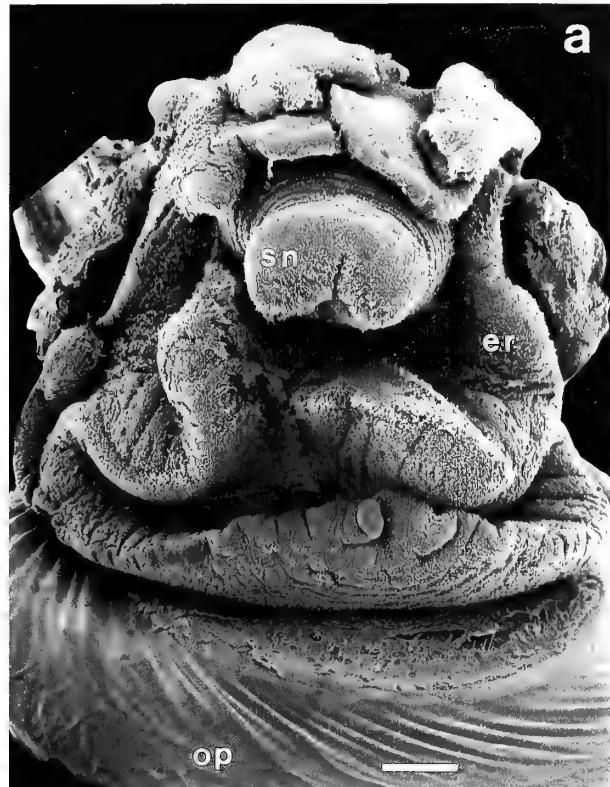
Material examined: JdF, Endeavour Segment: - ALVIN dive 2409, 1 young spm from a piece of flange (MNHN); - ROPOS HYS 364, 3 spms (V. Tunnicliffe ref. coll.); - Main Vent Field, 1 spm (FMNH 229661). Middle Valley: - ROPOS 149, 1 spm; - ALVIN dive 3146, 3 spms (FMNH 280952).

Distribution: Only known from the Endeavour segment, 2200-2250 m depth.

Etymology: "globularis," Latin, meaning globular.

Description: Shell (Figure 44a). Medium-sized for the group, globular, rather fragile, smooth, slightly yellowish beige by transparency of soft parts, with a very thin, slightly iridescent periostracum. The protoconch (Figure 37f) consists of about 0.8 whorls, diameter ca. 260 μ m, with a very small initial part sculptured by small, crowded pits, diameter 4-5 μ m, to some extent spirally arranged and fused. Where this sculpture ends, the diameter starts to increase rapidly and the shell becomes perfectly smooth. The outer lip of the protoconch is slightly constricted and its radial width is three times the width of the whorl where the sculpture stops. The teleoconch consists of about 2.5 almost perfectly smooth whorls; the precise number cannot be given because the half-grown and larger specimens have lost the apex by corrosion. The

Figure 45. *Hyalogyrina umbellifera* Warén & Bouchet, sp. nov., critical-point dried, Aleutian Seeps, Shumagin site. a. Frontal view. b. Right side of head-foot. c. Dorsal view of head-foot. d. Left side of head-foot. ct - cephalic tentacle; er - epipodial ridge; fe - edge of foot; op - operculum; sn - snout. Scale bars 0.2 mm.



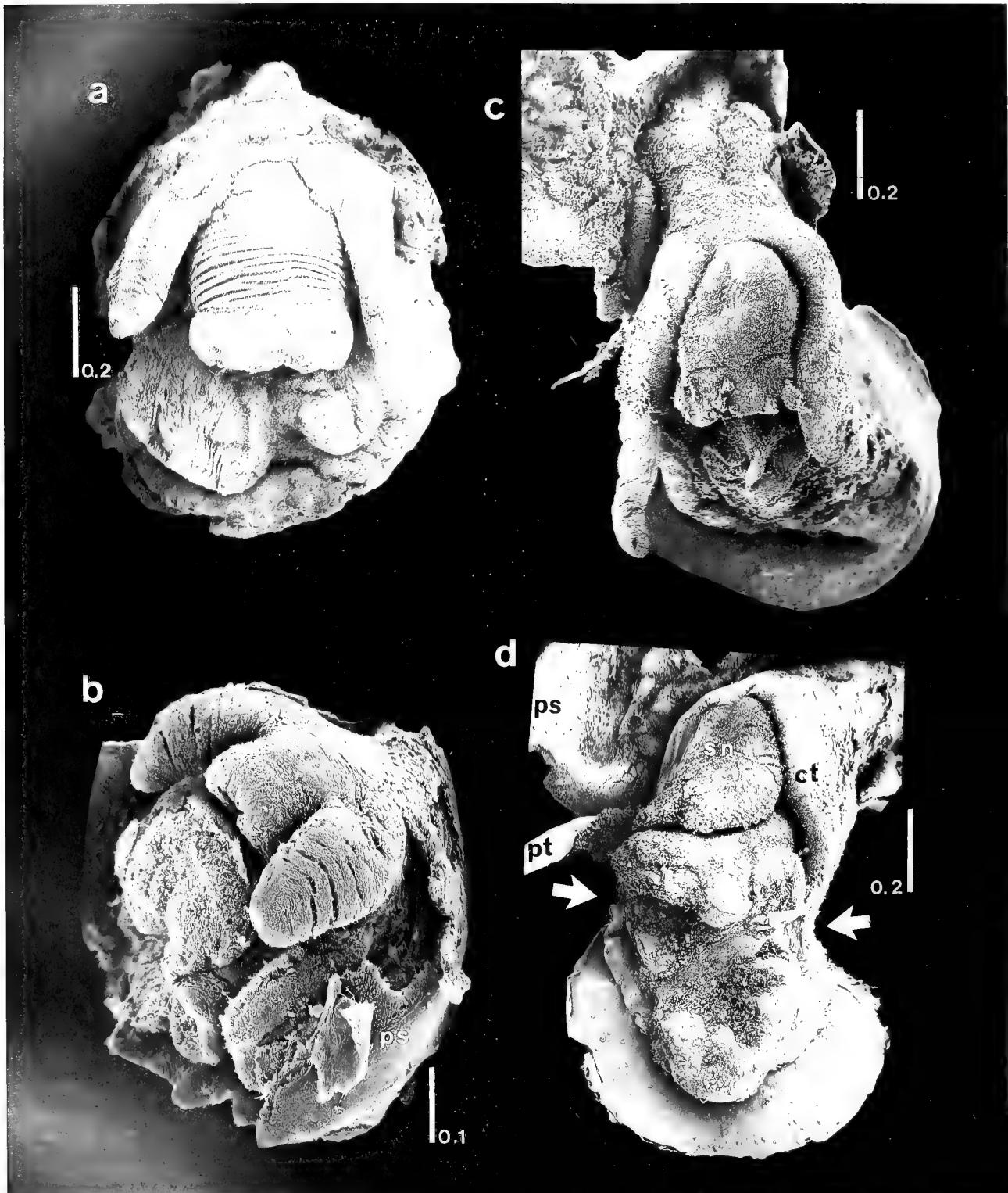


Figure 46. Critical-point dried soft parts. a. *Hyalogyrina globularis* Warén & Bouchet, sp. nov., paratype, FMNH. b. *Peltospira lamellifera*, EPR, 13°N. c. d. *Lurifax vitreus* Warén & Bouchet, gen. & sp. nov., paratypes. c. Dorsal view. d. Anterior view, foot partly autotomized, arrows indicate position of autotomy. ct - cephalic tentacle; f - foot; ps - pallial skirt; sn - snout; pt - pallial tentacle. Scale bars in mm.

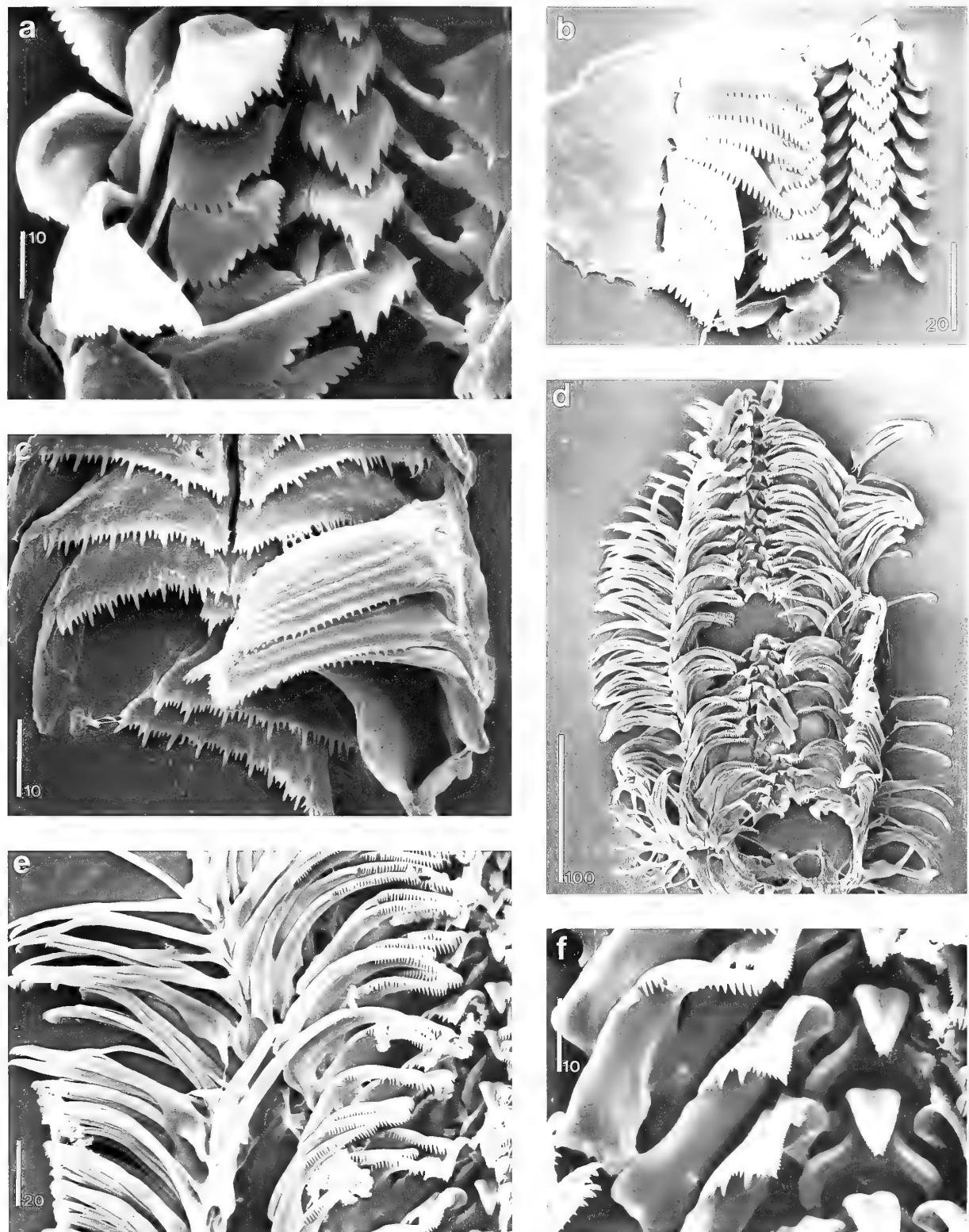


Figure 47. Heterobranchia, radulae. a, b. *Lurifax vitreus* Warén & Bouchet, gen. & sp. nov., paratype. a. Detail of central and lateral teeth. b. About half the length of the radula, laterals missing at right side. c. *Xylodiscula analoga* Warén & Bouchet, sp. nov., paratype. d. *Hyalogyrina umbellifera* Warén & Bouchet, sp. nov., Aleutian Seeps, Shumagin site, complete radula (see also Figures 48a–b). e, f. *H. globularis* Warén & Bouchet, sp. nov. e. Half width of radula. f. Detail of central and lateral tooth. Scale bars in µm.

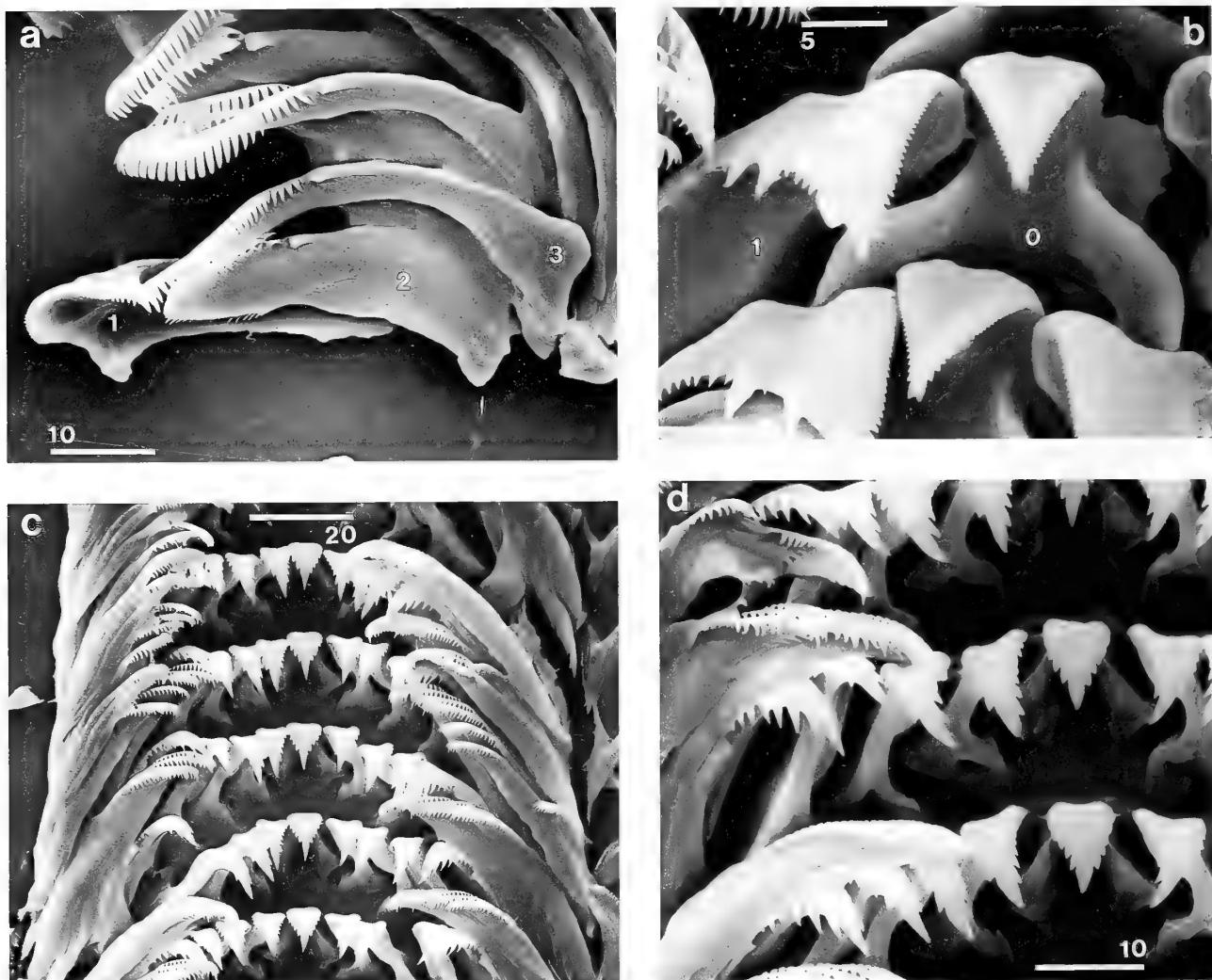


Figure 48. Radulae. Teeth numbered sequentially with central tooth as 0. *a, b.* *Hyalogyrina umbellifera* Warén & Bouchet, sp. nov., Aleutian Seeps, Shumagin site. *a.* First and second laterals, first marginal tooth. *b.* Central tooth and first lateral. *c, d.* *Peltospira lamellifera*, EPR, 13°N. *c.* Whole width. *d.* Detail of central field and inner marginals. Scale bars in μm .

suture is deep and the whorls not very firmly adjoined. The entrance to the umbilicus is quite oblique, and its width in a ventral view corresponds to $\frac{1}{15}$ of the diameter of the shell. The peristome is prosocline, more tangential than radial, not thickened, and not indented by the preceding whorl. The cross section of the whorls is almost circular.

Dimensions. Maximum height ca. 1.9 mm (holotype).

Soft parts (Figure 46a). The foot is large, broad and flat, posteriorly rounded, anteriorly shallowly bilobed, and lacking a demarcated propodium. The anterior corners are drawn out to short tentacles. An epipodial ridge starts at the anterior part of the operculum, continues forward and reaches the base of the cephalic tentacles. No epipodial tentacles. The cephalic tentacles are about as long as the snout in preserved specimens, and seem to be

smooth. They are connected by a small skin fold across the base of the snout. The right tentacle has a low, dorsal ridge at its basal $\frac{1}{5}$. The left cephalic tentacle has a similar ridge at its central side. The snout is almost cylindrical, strongly transversally folded, slightly expanded and ciliated distally, and has an apical-ventral mouth. The slender buccal mass is longer than the snout, with salivary glands opening to the buccal cavity, jaws composed of apically denticulate rodlets, and a short "rhipidoglossate" radula with simple, rounded end of the radular sac. The pallial cavity is rather deep, half a whorl, and the bipectinate gill is attached only at its basal part, behind the ctenidial leaflets. It is situated just in front of the intestinal coils, with the very low, ridgelike leaflets paralleling line of attachment. A large afferent vessel, is possibly connected to the rectal sinus. The afferent mem-

brane is attached just in front of rectum, the efferent one over in the far left part of pallial cavity. The pallial margin is distinctly thickened and has a densely ciliated tentacle at its right corner. The inner, posterior half of the cavity is filled by invaginated pallial roof, with a loop of the large intestine. The stomach and intestine contain grey sediment; in the intestine the fecal rod is partly split by a deep longitudinal furrow.

Operculum. Transparent, colorless; round, multispiral, with distinct growth lines. The width of the last whorl, at the growth zone, corresponds to $\frac{1}{5}$ of the diameter.

Radula (Figures 47e–f). Ca. 15 - 1 - 1 - 1 - ca. 15, short, 3–3.5 times as long as broad, rhipidoglossate, with marginal teeth folded across laterals and central. The central tooth is low and broad with projecting lateral supports, a triangular, finely serrated apical plate and distinct “wings” behind the lateral support. The lateral tooth is low and broad, its central half forms a triangular plate with finely serrated central side and a more coarsely denticulate outer side with irregularly scattered larger denticles. Its outer half is simple, and lacks dentation. The first marginal is flattened, with a dorsal regular comb of small denticle, an apical finely serrated truncation, and an equally fine ventral serration. The basal $\frac{1}{3}$ of its length lacks serration. The second marginal is longer, more slender, and both sides of the apical half are denticulate. Laterally the teeth become slightly shorter, more slender, and lose the denticles.

Jaw. Bipartite and consists of numerous rods in a tielike arrangement and equipped with three to five denticles at their free (inner) end.

Remarks: *Hyalogyrina globularis* resembles *H. grassei* Warén & Bouchet, 1993, from the Guaymas Basin, but has a more globular shape, more slowly increasing diameter of the whorls, and the shell has a proportionally larger aperture. We do not know if the poor development of the cephalic tentacles (compared with *H. umbellifera*) is because our specimens are young, or if there is much variation in this character within the group. *Hyalogyrina grassei* has the same arrangement of the cephalic tentacles as *H. globularis*.

Family ORBITESTELLIDAE Iredale, 1917

Remarks: The genus *Orbitestella* Iredale, 1917, contains mainly shallow water species, usually living under rocks (Ponder, 1990; Bosch et al., 1995; own observations). A second genus, *Microdiscula* Thiele, 1912, is restricted to shallow water in the temperate parts of Australia and off Antarctica in deeper water. (The third genus, *Boschitestella* Moolenbeek, 1994, is very similar to *Orbitestella*, and we feel uncertain about the necessity for it.)

The new species below shares some shell characters with *Orbitestella* (*Microdiscula* has a smooth shell), but

is three times as large as the average species of *Orbitestella*. The protoconch of *Lurifax* shows no trace of heterostrophy despite being multispiral, and the shape of the shell differs from orbitestellids by having a distinct spire (not planispiral). The sculpture consists of fine spiral and axial cords, not mainly broad, rounded axial ridges. The radula, however, is indistinguishable from that of *Orbitestella* and *Microdiscula*, and we feel sure about the family assignment.

Lurifax Warén & Bouchet, gen. nov.

Type species: *Lurifax vitreus*, sp. nov.

Diagnosis: Orbitestellids with unusually tall-spired and large shell with fine sculpture of spiral ribs and keels of variable strength and radiating flexuous incremental lines. Umbilicus deep. Protoconch of 1.5 smooth whorls. Radula normal for family.

Etymology: “lurifax,” Swedish, a person who tries to deceive, referring to the confusing shell morphology. Gender masculine.

Remarks: The name of this new genus and species is well deserved; at the first sorting, specimens with poorly developed spiral sculpture fooled the senior author that they were a species of *Leptogyra* Bush, 1897 (Vetigastropoda), those with developed spiral sculpture that they belonged to *Cyclostremiscus* Pilsbry & Olsson, 1945 (Neotaenioglossa).

A very similar species was reported by Lewis & Marshall (1996) from a seep off New Zealand as *Pterolabrella* sp. The latter genus is based on a New Zealand Tertiary fossil species, most likely belonging to the Vitrinellidae. The specimens from New Zealand do, however, fit better in *Lurifax* (Marshall, personal communication).

Lurifax vitreus Warén & Bouchet, sp. nov.

(Figures 37c, d, 44e–g, 46c, d, 47a, b)

Type material: Holotype and 55 paratypes in MNHN.

Type locality: MAR, Menez Gwen, DIVA 2 PL 11, 37°50.54'N, 31°31.30'W, 860–870 m, on mussels.

Material examined: MAR, Menez Gwen: - DIVA 1 PL 13, on an active chimney, 9 spms; - DIVA 1 PL 14, on sulfide rock with Hydrozoa, 12 spms; - DIVA 1 PL 16, on base of a black smoker, 12 spms; on chimney, 2 spms; - DIVA 2 PL 14, suction sample among mussels, 1 spm; - DIVA 2 PL 16, 1 spm; - MARVEL PL1202, 850 m, retrieval box, 1 spm; - MARVEL PL1203, 850 m, retrieval box, 2 spms; - MARVEL PP46, particle trap, 1 spm. *Lucky Strike*: - DIVA 1 PL 04, in baited trap, 2 spms; with mussels and polychaetes, 4 spms; on inactive chimney among Hydrozoa and sponge *Cladorhiza*, 32 spms; - DIVA 1 PL 08, on a rock, 1 sh; - DIVA 1 PL 17, among

mussels, 5 spms; - DIVA 1 PL 19, among mussels, 1 spm; - DIVA 2 PL 02, 6 spms; - DIVA 2 PL 03, 10 spms; - DIVA 2 PL 04, 5 spms; suction sample among mussels in shimmering water, 3 spms; - DIVA 2 PL 07, 31 spms; 2 suction samples among mussels and hydrothermal sediments, 8 and 8 spms; - DIVA 2 PL 08, retrieval box, 3 spms; - DIVA 2 PL 09, 14 spms; - DIVA 2 PL 10, 13 spms; on a rock, 8 spms; retrieval box, 189 spms; - DIVA 2 PL 19, 3 spms; - DIVA 2 PL 20, 2 spms; - DIVA 2 PL 21, 1 spm; - DIVA 2 PL 26, 1 spm; - ALVIN dive 2604, 1 spm; - ALVIN dive 2607, 21 spms; - LUSTRE Exp., Tour Eiffel, on mussels, 1 spm; - MARVEL PL1193, Tour Eiffel, retrieval box, 4 spms; - MARVEL PL1194, Tour Eiffel, retrieval box, 5 spms.

Distribution: MAR, from Menez Gwen to Lucky Strike, ca. 850–1800 m depth, seems to be epifaunal.

Etymology: “*vitreus*,” Latin, referring to the transparent shell in well preserved specimens.

Description: Shell (*Figures 44e–g*). Large for its family, vitrinellidlike, depressed conical, rather fragile, vitreous, often covered by thick crusts of rust. The protoconch (*Figure 37c, d*) consists of ca. 1.5 perfectly smooth whorls of slowly increasing diameter, sculptured by faint incremental lines, without a trace of heterostrophy, diameter 300–310 µm. The teleoconch has up to 3.5 whorls of slowly increasing diameter, sculptured by collabral, sharp, dense, and flexuous incremental lines. The spiral sculpture consists of numerous spiral striae of which those between the shoulder and periphery may develop into stronger ribs and give the shell a keeled appearance. The aperture is rounded-rhombic, distinctly broader than high, the peristome is not thickened. The umbilicus is broad and deep.

Dimensions. Maximum diameter 2.8 mm.

Soft parts (*Figures 46c, d*). The foot is long and slender, anteriorly truncated, posteriorly tapering, with well demarcated propodium. There are no appendages except the metapodial lobes. The head has a pair of simple cylindrical cephalic tentacles, each with a well developed eye dorsally in the base. Pallial margin with at least one well developed, ciliated pallial tentacle attached just inside the right corner.

Oberculum. Multispiral with about six whorls, central nucleus, weak incremental lines, stiff, almost transparent.

Radula (*Figures 47a, b*). 1 - 1 - 1 - 1 - 1. The central tooth has an apical, rhombic, serrated plate and widely diverging antero-lateral supports. The lateral tooth has an ovate, irregularly serrated plate with an antero-lateral basal process. The marginal tooth consists of a long, triangular plate with short base and anteriorly serrated margin.

Jaw. Not examined in detail, consisting of numerous small elements.

Remarks: *Lurifax vitreus* often autotomizes the posterior part of its foot when being preserved (*Figure 46d*). This

is not known for shallow water species of *Orbitestella*, but may be a response to predators grabbing the foot.

The shell of *Lurifax vitreus* is amazingly similar to species of *Cyclostremiscus*, a genus of the neotaenioglossate (Caenogastropoda) family Vitrinellidae, but the radula and soft parts convincingly show that it belongs to the Orbitestellidae.

Family XYLODISCULIDAE Warén, 1992

Xylodiscula Marshall, 1988

Xylodiscula Marshall, 1988:988.

Type species: *X. vitrea* Marshall, 1988; by original designation; deep water off New South Wales, on sunken drift wood.

Remarks: The genus now includes seven species. Two are known from hydrothermal vents, three, perhaps four (Hasegawa, 1997) from sunken drift wood, and two from accumulations of *Posidonia* fibers (Warén & Bouchet, 1993). The two species from hydrothermal vents differ by being about twice the size of those from non-vent localities.

Xylodiscula analoga Warén & Bouchet, sp. nov.

(*Figures 44b–d, 47c, 49h*)

Type material: Holotype in MNHN.

Type locality: MAR, Lucky Strike, ALVIN dive 2607, 37°17.50'N, 32°16.47'W, 1628 m, Sintra site.

Material examined: MAR, Menez Gwen: - MARVEL PL1201, 850 m, 5 spms; - MARVEL PL1202, 850 m, retrieval box, 2 spms; - MARVEL PL1203, 850 m, retrieval box, 1 spm; - MARVEL PP46, particle trap, 1 young. *Lucky Strike*: - DIVA 1 PL 19, among mussels, 2 spms; - DIVA 2 PL 07, 1 spm.

Distribution: Only known from the material above, MAR from Menez Gwen to Lucky Strike, 850–1728 m depth.

Etymology: From “*analogos*” (Greek), meaning similar.

Description: Shell (*Figures 44b–d*). Large for the genus, fragile, with a thick yellowish, brownish periostracum, subplanispiral, with whorls of round cross section and rapidly increasing diameter. Protoconch not seen, corroded in all specimens. The teleoconch has about 2.5 whorls of round cross section, not indented by preceding whorl and sculptured only by collabral incremental lines. The aperture is subradial and slightly prosocline, slightly flexuous in profile. The umbilicus is deep and wide.

Dimensions. Maximum diameter of holotype 1.7 mm, maximum diameter examined ca. 3 mm.

Oberculum (*Figure 49h*). Thin and transparent, round, smooth, multispiral with central nucleus.

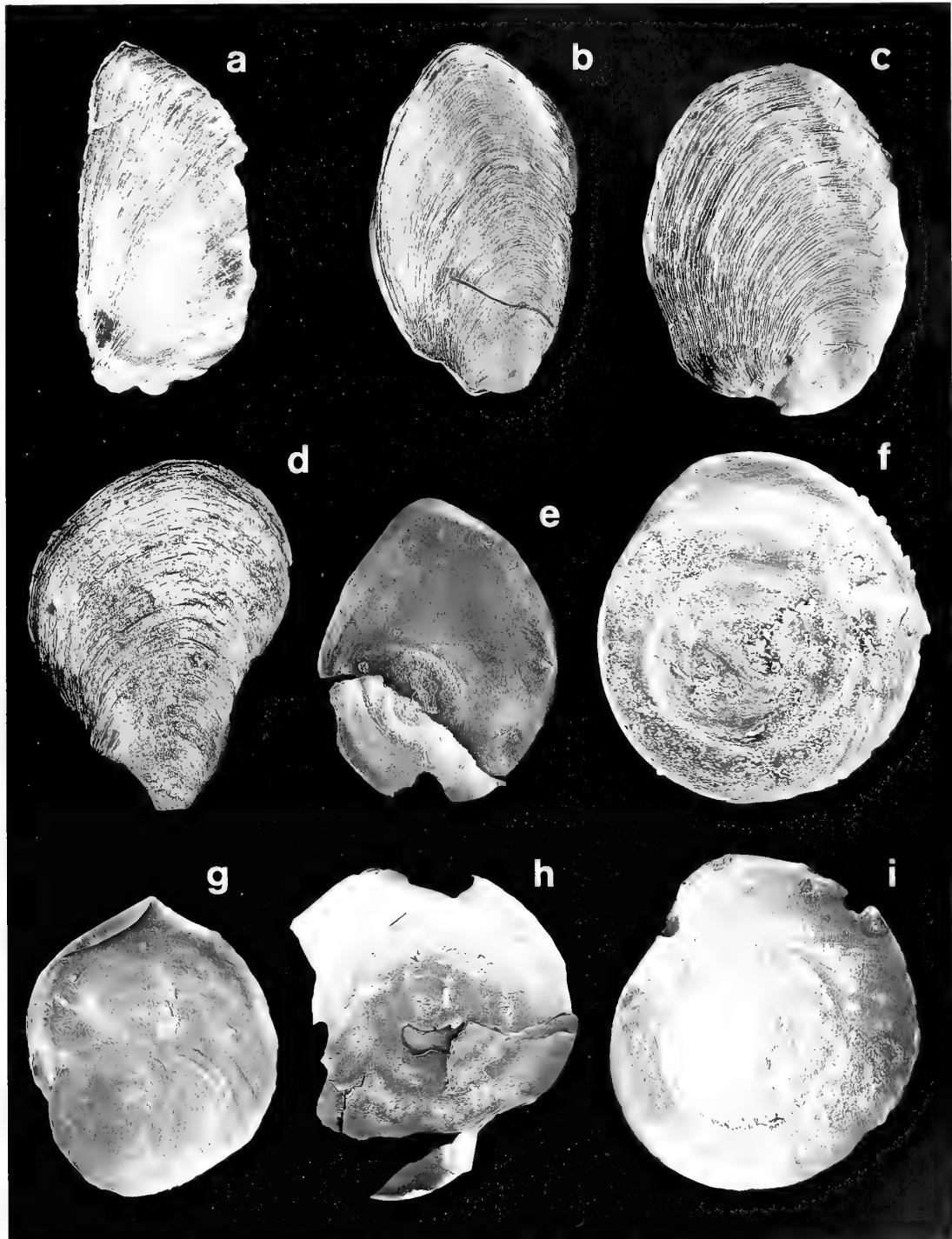


Figure 49. Opercula. *a. Eosipho auzendei*, Warén & Bouchet, sp. nov., paratype, diameter 18 mm. *b. E. canetae*, Bush Hill Seep, diameter 11.4 mm. *c. Bayerius arnoldi*, Aleutian Seeps, Edge site, diameter 7.5 mm. *d. B. peruvianus* Warén & Bouchet, sp. nov., paratype, diameter 7.7 mm. *e. Laeviphitus desbruyeresi* Warén & Bouchet, sp. nov., MAR, Lucky Strike, diameter 0.7 mm. *f. Neusas* Warén & Bouchet, gen. nov., *marshalli*, MAR, Menez Gwen, diameter 0.55 mm. *g. Speculator cariosus* Warén & Bouchet, gen. & sp. nov., holotype, diameter 1.6 mm. *h. Xylodiscula analoga* Warén & Bouchet, sp. nov., paratype, diameter 0.8 mm. *i. Hyalogyrina umbellifera* Warén & Bouchet, sp. nov., Aleutian Seeps, Shumagin site, diameter 1.0 mm.

Radula (Figure 47c). 1 - 1 - 0 - 1 - 1, short and broad with about 20 transverse rows of teeth. The marginal teeth are roughly triangular, long, and finely serrated along the anterior edge. The lateral teeth are broadly triangular with a projecting lateral support; their anterior edge is serrated with nine or 10 larger, cylindrical and pointed denticles with irregular interspaces and one to four much smaller ones between each pair of the larger ones.

Remarks: *Xylodiscula major* Warén & Bouchet, 1993, the other species of this genus known from hydrothermal vents, has a flatter shell with whorls of more slowly increasing diameter, its radula has much more slender marginal teeth, and the serration of the laterals consists of teeth of uniform size.

DISCUSSION

Tunnicliffe et al. (1998) presented a thorough discussion of the biogeography and related topics of the hydrothermal vent fauna. We have previously discussed several aspects of the gastropod fauna of the vent and seep environments (Warén & Bouchet, 1989, 1993) and will here restrict these discussions to a few comments on the vent environment. The mollusk fauna of the seeps is intermediate between the faunas of vents and those of the surrounding deep-sea (Warén & Bouchet, 1993; Tunnicliffe et al., 1998) with a few large, endemic, chemosynthetically nourished animals that constitute the majority of the biomass, for example species of *Bathymodiolus* or vesicomyids (*Bivalvia*) or Vestimentifera (Sahling, 1997; Carney, 1994; Jollivet et al., 1990; Suess & Bohrmann, 1997).

The aspects for which we feel that the new information is sufficient to complete earlier discussions are distribution, endemism, and age of the fauna of the hydrothermal vents.

Distribution. Appendix 1 updates Warén & Bouchet's (1993) list of seep and vent localities from which gastropods have been reported. It also gives a summary of the fauna of each locality. From these lists it is very clear that each of the three well documented areas, JdF, EPR, and MAR, has a fauna of its own with no overlap. The following comments are needed:

MAR. A uniform fauna with 15 species occurs from 38°N to 14°45'N along the MAR. We have identified some species from Menez Gwen, the northernmost of the sites, with a main distribution outside the vents. Most of these are well known from normal bathyal environments, but three species (*Neusas marshalli* (1 record), *Alvania stenolopha* nine records) and *Rokopella segonzaci* (one record)) are of uncertain status. These are not included in the 15 spp.

JdF Ridge system. The Gorda Ridge off northern California (41°N) still is poorly known (six spp. identified), but seems to resemble the northern localities much more

than the EPR (see Warén & Bouchet, 1993:87). Three species of the main system (44–50°N), *Provanna laevis*, *P. variabilis*, and *Pyropelta musaica* are also known from the seeps off Oregon and the Guaymas Basin. *Buccinum viridum* Dall, 1890, was described from (seeps?) off Santa Barbara, California, but no details about this locality are known, and the identification of the specimens from JdF is uncertain (McLean, personal communication). No other species out of the 14 species known from JdF are known elsewhere, although the Oregon seeps are nearby.

EPR and Galapagos Rift. A very uniform fauna with about 35 endemic species occurs along the EPR, from 21°N to 17°S. Of 16 species collected at 17°S, 14 are known also at the more northern localities. The Galapagos rift fauna has 11 species of gastropods of which *Lacunoides exquisitus* is not known from other localities; otherwise the species are known also from the EPR. There is no overlap with the seep fauna of the Guaymas Basin, or the seeps off Peru. Three additional species (*Moelleriopsis* sp., *Sinezona* sp., *Falsimargarita naudurii*), are known from a single specimen each and may be occasional intruders.

Western Pacific vents. These are more difficult to compare with each other since the Japanese vents have been less thoroughly reported from a biological point of view, and few gastropods have been reported from more than a single locality. The same is true for the Edison Seamount vents (ca. six spp. known; Tunnicliffe, 1994; Beck, 1996; Warén & Bouchet, herein). The Manus Back Arc Basin has been more investigated (Beck, 1992a, b, 1993; Galkin, 1993). The Mariana Back Arc Basin is represented by six species of which four are known from there only. The North Fiji and Lau Basins are better known, with altogether 30 species (Warén & Bouchet, 1993; Okutani & Ohta, 1993; Beck, in press). About 50% of these are shared between the two localities. Three species are shared between at least two of the Manus, Mariana, and Fiji basins: *Lepetodrilus schrolli*, *Alviniconcha hessleri*, and *Ifremeria nautilae*. In some further cases there are closely resembling species in two or three of these localities:

Symmetromphalus hageni (Manus), *regularis* (Mariana) and *macleanni* (Fiji)

Shinkailepas conspira (Fiji), *tufari* (Manus)

Pyropelta ovalis (Fiji), *bohlei* (Lihir)

Pseudorimula leisei (Fiji), *marianae* (Mariana)

In the case of *Alviniconcha* genetic differences between the populations in the Lau and North Fiji Basins were reported by Denis et al. (1993), but considering that the specimens are morphologically inseparable we find it premature to assume that two species are involved, and in any case the similarity must indicate recent connections between the localities.

We therefore assume that there is more faunal relationship between the western Pacific vent systems than with other vent systems.

An analysis of the genus level relations between the four major vent systems shows that a few genera like *Provanna* (absent from MAR), *Lepetodrilus* (present at all), and *Phymorhynchus* (present at all?) are quite widely dispersed. Other genera may occur at widely scattered localities: *Pseudorimula* (WP - MAR), *Shinkailepas* (WP - MAR), *Peltospira* (EPR - MAR), *Fucaria* (JdF - WP; also seeps off Florida), *Lurifax* (MAR and seeps off New Zealand). This disjunct distribution may be a result of missing information, but it may also indicate that the gastropods have a good dispersal capacity.

Some genera have a rather restricted distribution at vents and seeps:

Buccinum, *Neptunea*, and *Oenopota* occur at North Pacific vents and seeps, but have their main distribution in shallow, non-vent environments.

Gorgoleptis (three spp. EPR), *Nodopelta* (three spp. EPR), and *Desbruyeresia* (three spp. WP) have a few species each, they are restricted to a single vent system, and may represent local radiations.

Endemism. Knowledge on the extent to which the hydrothermal vent fauna is restricted to the vents is severely hampered by lack of knowledge on the normal deep-sea fauna, especially that of the bathyal and abyssal rocky bottoms and in the Pacific basins. There is also a problem with the vent fauna in general in that less than 25% of the species are known from more than one site (Tunnicliffe et al., 1998). The corresponding figure for gastropods is 55% known from more than one site. Nevertheless, some conclusions may be drawn, especially based on the fauna of the MAR vents, since the gastropod fauna of the surroundings there is much better known than in the Pacific.

Endemism at Species Level. Our knowledge on the gastropod fauna of the three well known localities at the MAR (Table 1; Menez Gwen, Lucky Strike, and Snake Pit) is based on 70 dives during which 1–10 samplings were made. Three such samples at Menez Gwen contained nine specimens and shells of six species well documented from non-vent environments (DIVA 1 PL 13-6; DIVA 2 PL 11, DIVA 2 PL 13). This shall be contrasted with ca. 500 specimens of eight species known from vents only in the same samples. It seems thus quite obvious that these samplings touched areas less affected by hydrothermal effluents, where conditions allowed species not acclimatized to vent life, to enter. Two subsamplings from Menez Gwen (DIVA 2 PL 11: *Pseudosetia azorica* and *Rokopella segonzaci*; DIVA 2 PL 26: *Neusas marshalli*) gave six specimens of three species; we do not know if they are a part of the vent fauna or not.

The most common and regularly occurring not endemic species at the MAR vents is *Protolira thorvaldssoni*. It was described from two specimens found on a piece of whale bone in a few hundred meters depth, south of Iceland. The shell is simple, the radula variable, and the external morphology of the soft parts is not known in the

Table 1.
List of species from MAR.

Species	Number of specimens
<i>Paralepetopsis ferrugivora</i> , sp. nov.	24
<i>Protolira valvatooides</i>	8895
<i>Protolira thorvaldssoni</i>	3855
<i>Sutilizona pterodon</i> , sp. nov.	17
<i>Lepetodrilus atlanticus</i> , sp. nov.	41,477
<i>Pseudorimula midatlantica</i>	257
<i>Peltospira smaragdina</i> , sp. nov.	766
<i>Lirapex costellata</i> , sp. nov.	45
<i>Shinkailepas briandi</i> , sp. nov.	1632
<i>Laeviphitus desbruyeresi</i> , sp. nov.	63
<i>Alvania stenolopha</i>	49
<i>Phymorhynchus ovatus</i> , sp. nov.	53
<i>Phymorhynchus moskalevi</i>	78
<i>Phymorphynchus carinatus</i> , sp. nov.	8
<i>Lurifax vitreus</i> , sp. nov.	492
<i>Xylodiscula analoga</i> , sp. nov.	13
Total	57,724

type material. Therefore there is some uncertainty in the identification, but at least the whale bone and vent specimens are closer to each other than to any other specimens we have seen.

A second case is *Alvania stenolopha*. About 50 specimens, from Menez Gwen and Lucky Strike, were found among 57,000 specimens of gastropods from the MAR.

No other species from the MAR vent fauna is suspected to occur also outside the vent environment.

Our material from the EPR at 13°N, the best known locality, includes ca. 35 species represented by about 325,000 specimens. Of these a single specimen each of three species does not belong to the vent fauna.

This can be summarized as species numbers: About 125 species of gastropods have now been identified from hydrothermal vent localities in the Atlantic and Pacific oceans. Six of these species are also known from localities outside the vents: *Alvania stenolopha* (MAR) and one species of *Buccinum* (*viridum*?, JdF) are known from undefined (non-vent?) environments. Four further species are known from hydrocarbon seeps (*Provanna laevis* and *Neolepetopsis gordensis*) and whale bone (*Pyropelta musaica* [Guaymas Basin and off Oregon] and *Protolira thorvaldssoni* [MAR]). These six species are regular component of the fauna, each known from a few to several records in vent environments. However, four of the six species are in one way or another connected with taxonomic problems and it is only *Alvania stenolopha* and *Provanna laevis* for which we are convinced that the records outside hydrothermal vents are conspecific.

This means that 95–98% of the fauna is endemic at species level. That is a slightly higher figure than given

by Tunnicliffe et al. (1996), 93% for the fauna in general, in the vent environment.

Genus Level. About 57 genera of gastropods are known from hydrothermal vents; 31 (54%) are endemic; eight further genera occur also in various kind of seeps, but are not known from non-chemosynthetic environments. If these are included, 70% of the genera in hydrothermal vents are endemic to chemosynthetic environments.

Family Level. Among the families, Peltospiridae (nine genera, 17 species) and Sutilizonidae (three genera, six species) are endemic; Neomphalidae (nine genera, 15 species [one in seeps, *Retiskenea diploura*]) and Lepetodrilidae (four genera, 20 species [one in seeps, *Lepetodrilus guaymasensis*]) are almost endemic to vents. The families Provannidae (four genera, 12 species in vents, eight in seeps, one in both) and Neolepetopsidae (three genera, six species in vents, two in seeps and one in both) are also taxa that have their main distribution in vents. Together these families have an average of 5.3 genera and almost 12 species per family living in the vents. This shall be compared to 1.3 genera and 2.4 species per family among the ca. 25 (23–27 depending on family concept) families mainly known from outside the vents. From these figures it is obvious that the families which have their main distribution in the vents also have undergone a considerable radiation there. These are also the families that exhibit many morphological adaptations and of which the relations are difficult to recognize. This problem directly leads to the next question, the “age” of the vent fauna.

Age and Origin of Vent Gastropod Fauna. It has been suggested that the hydrothermal vents have acted as refugia for Palaeozoic-Mesozoic faunas, and that the vents have been quite isolated since the time they were first inhabited. For non-mollusk taxa, the first evidence of antiquity of vent animals was given for a stalked barnacle (Newman, 1979), which was considered intermediate between a genus known only from the Upper Triassic and another known from Jurassic until Recent. Newman (1985) elaborated this idea and discussed further invertebrates, among them also gastropods, and considered the higher endemic taxa (families etc.) to be relicts of Palaeozoic and Mesozoic age. These opinions have then been supported by Král (1995), Tunnicliffe (1991), Tunnicliffe & Fowler (1996), Tunnicliffe et al. (1996), Tunnicliffe et al. (1998), McArthur & Tunnicliffe (1998).

McLean has in several papers emphasized a Palaeozoic to Lower Mesozoic origin of endemic gastropod families: Lepetodrilidae (1988), Peltospiridae (1989b), Neomphalidae (1990b) and Neolepetopsidae (1990a), but this has only in the case of Neolepetopsidae been supported by direct reference to a similar fossil taxon, assumed to be related at superfamily level. Also Beck (1992a, b, 1993, 1996) has in several, more cursory comments suggested an ancient origin of vent gastropods.

The mollusks in general and especially the marine gas-

tropods have an excellent fossil record compared with other groups of invertebrates. This helps to give some ideas about the age of many of the major taxa of gastropods. On the other hand, the richness of fossils also gives good opportunities for erroneous conclusions because of convergence in shell characters. This is especially obvious with simplified shells, like many of the species of the vent fauna.

Table 2 summarizes the present knowledge on the earliest appearance of families or reliably identified lower taxa from hydrothermal vents. Most information here is of little value; many of the taxa consist of small species with featureless shells and may occur unnoticed in earlier deposits. For others, e.g., Fissurellidae, Trochidae, and Turbinidae, the table gives a more reliable idea of the earliest appearance of the taxon, but nothing is known about when the vent-inhabiting subtaxon entered hydrothermal vents. The families Conidae and Buccinidae are, however, more informative. These two families (with 13 species and five genera in vents) go back to the Late Cretaceous only. The species were then large and common, but cannot be recognized in Early Cretaceous deposits. In the case of the genus *Buccinum*, with two species, one in vents and one in seeps, an even more recent and precise maximum age can be given since the oldest species is from the Late Oligocene (Golikov, 1980). For *Neptunea* (one species at the Kaikata Seamount vents) a Late Eocene age has been given (Strauch, 1972). The case is similar for *Phymorhynchus*; the earliest appearance of its subfamily is Eocene. This clearly shows that some immigration into the hydrothermal vents has taken place in quite recent time, Late Cretaceous to Eocene; for *Buccinum* even Late Oligocene, and that the vent environment is not completely isolated.

Among the four major endemic vent radiations, Neolepetopsidae, Lepetodriidae, Peltospiridae, and Neomphalidae, the three latter taxa show considerable variation in their morphology, which has been used as evidence that they have lived isolated in the vent environment for a long time (back to Late Palaeozoic or Early Mesozoic). This assumption is contradicted by the fact that within each of these taxa, there is virtually no variation in protoconch characters (Lepetodriidae, see Warén, in press; Peltospiridae and Neomphalidae, see Warén & Bouchet, 1989, 1993, and herein). All other non-vent vetigastropod families and subfamilies show a considerable variation in this character, often also within a genus. Warén (in press), based on an analysis of the Lepetodriidae and related non-vent groups, suggested a maximum age of Late Triassic for this superfamily. The radiation may, however, as well be of Late Mesozoic or Caenozoic origin, since the tree could not be resolved between Scissurellidae, Haliotidae, and Lepetodriidae. The sister taxa Scissurellidae and Haliotidae go back to the Jurassic and Late Cretaceous respectively. McArthur (1999) suggested “at least mid-Mesozoic” origin for Neomphalina (Peltospir-

Table 2.

Fossil record of gastropod taxa from hydrothermal vents. Data mainly from Tracey et al. (1993), Moore (1960) and Wenz (1938–1944), supplemented by more recent information when available.

Taxon	Earliest known fossil record//Recent distribution
Cocculiniformia	Eocene//mainly bathyal biogenic substrata
Hyalogyrinidae	Oligocene (Lozouet, 1997)//bathyal to shallow biogenic substrates
Orbitestellidae	Eocene (Ducasse et al., 1973)//bathyal to shallow
Xylodisculidae	Late Eocene? (Warén & Bouchet, 1993:53)//bathyal to shallow biogenic substrates
Cerithiopsidae	Jurassic (Dogger) (Gründel, 1980)//sponge feeders
Elachisiniidae	Paleocene//shallow water
Provannidae	Late Jurassic (Campbell, unpublished), Late Eocene (Squires, 1995)//in seeps and on driftwood
Rissoidae	(Jurassic?) Cretaceous//all abyssal to littoral environments
Vitrinellidae	Cretaceous//all bathyal to littoral environments
Conidae	Cretaceous//all abyssal to littoral environments
Buccinidae	Cretaceous//all abyssal to littoral environments
<i>Buccinum</i>	Late Oligocene//north Pacific, Atlantic and Arctic, bathyal to littoral
<i>Neptunea</i>	Late Eocene//north Pacific, Atlantic and Arctic, bathyal to littoral
Neomphalina	Late Eocene seeps, Warén & Bouchet herein//endemic to vents and seeps
Neritoidea	Late Triassic//Recent non-vent species in shallow, marine to fresh water environments
Acmaeidae	Mid Triassic//mainly in shallow water
Neolepetopsidae	no fossils known, compared to Lepetopsidae (Permian-Triassic) (McLean, 1989)
Peltospiridae	no fossils known (McLean, 1990b); Late Jurassic-Early Cretaceous (?) Campbell, pers. comm.)//endemic to vents and seeps
Fissurellidae	Triassic (Bandel, pers. comm.)//all abyssal to littoral environments
Lepetodrilidae	no fossils known, McLean (1988)//endemic to vents and seeps
Sutilizonidae	Not known as fossil//endemic to vents
Skeneidae	Cretaceous(?)//all abyssal to littoral environments
Trochidae	Triassic(?)//all abyssal to littoral environments
Turbinidae	Triassic(?) (Permian???)//all bathyal to littoral environments

idae + Neomphalidae) based on molecular information, but their comparison included almost no freeliving possible relatives.

The ages given in Table 2 do not differ drastically from

those that would be obtained for any other marine gastropod assemblage, and groups like Neritimorpha, Fissurellidae, Trochidae, and Acmaeidae (all of Triassic origin) are common in many non-vent environments (quoting some of the oldest ones).

Fossil hydrothermal vents are well known back to the earliest Palaeozoic times (Little et al., 1997, 1998), but it is rare that they contain fossils well enough preserved to allow any conclusions about the inhabitants. This is largely a result of the vent environment, with an outflow of hydrothermal fluids with a pH of 2–6, and richness of decaying organic material. Almost all empty shells of gastropods recovered from modern vents consist mainly of periostracum, and even adult living specimens are often severely attacked (Figure 42c).

Fossil vents with “identifiable” animal remains have been described back to the Silurian (Little et al., 1997, 1998, 1999a, b), and gastropods have been tentatively identified as members of the family Nododelphinulidae in the Jurassic (Little et al., 1999a) and as cerithioids and epitoniids in the Cretaceous (Little et al., 1999b). Apart from these attempts, it has generally not been possible to identify gastropods to family level. Deposits from seep communities are better known, and gastropods have been identified, in some cases belonging to genera known from modern vents and seeps (Moroni, 1966; Squires & Goedert, 1991; Goedert & Squires, 1990; Taviani, 1994; *?Sahlingia*: Squires & Goedert, 1996 [as *Thalassonerita*]; *Provanna*: Squires, 1995; and its relative *Abyssochrysos*: Goedert & Kaler, 1996; *Retiskenea*, Goedert & Benham, 1999).

The bivalves also show a similar pattern. Campbell & Bottjer (1993, 1995) showed that during the Late Jurassic bivalves of the families Vesicomyidae, Mytilidae, Lucinidae, Thysiridae, and Solemyidae began to replace brachiopods in seeps and vents, to become dominant in the Early Cretaceous. The genera *Vesicomya* and *Calyptogena* (Vesicomyidae) which dominate many seeps and vents are known as fossil back to the Late Eocene in methane seeps (Goedert & Squires, 1990). (Earlier reports about Silurian vesicomyids [Kuznetsov et al., 1993] were based on misidentified brachiopods (!) [Little et al., 1997]). In Eocene and Miocene seeps there were mussels more similar to *Modiolus* (Moroni, 1966; Squires & Goedert, 1991), instead of the genus *Bathymodiolus*, which now often dominates in vents and seeps.

We therefore favor a view that throughout the times during which vents have existed, there has been a continuous immigration of new taxa from more shallow water, often via seeps and biogenic substrates, with concomitant extinction of taxa already living in the vents. A result of this model is that the taxa of the vent (and seep) fauna will be slightly older than those of shallow water, but from there to a relict fauna of Palaeozoic-Mesozoic origin, there is a long step.

A consequence of this view is that it is likely that some

of the palaeontologically “old” taxa with few and rare species in vents, like the grazing species of *Puncturella* may be the last surviving “dinosaurs” in the process of losing the competition with the presumed more efficient, and presumably more recently evolved gastropods (e.g., lepetodriloids), which combine grazing with filter-feeding or bacterial symbiosis. It seems unlikely that, confronted with an inflow of taxa with newly evolved functional specializations, the old and original immigrants should have resisted competition throughout 400 million years.

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- Note Added in Proof**
- While this paper was in press, several papers were published that affect the discussion on age, origin, and distribution of the fauna.
- Based on sequences of mtDNA of *Alviniconcha* from four different populations, Kojima et al. (1998) expanded the results of Denis et al. (1993), based on allozyme frequencies, and concluded that three species are present in the western Pacific back-arc basins: *A. hessleri*, restricted to the Mariana Trough, *Alviniconcha* sp. A, in the Manus and North Fiji Basins, and *Alviniconcha* sp. B, in the North Fiji and Lau Basins. Possibly, a finer morphometric re-analysis of the shells is needed.
- Bandel & Kiel (2000) have described *Desbruyeresia antiqua* from the Campanian (Late Cretaceous) of Spain. They rejected a position of Provannidae in the Loxomatoidea because *Loxonema* Phillips, 1842, is “most probably” a member of the Archaeogastropoda, and instead place the family in the superfamily Cerithioidea. Even if this is the case, the similarities in protoconch morphology between Provannidae and Pseudozygopleuridae remain, and we hypothesize that the relationship of Provannidae is with Zygoeuroidea rather than with Cerithioidea. The Zygoeuroidea are considered paraphyletic by Nützel (1998) and represent a grade rather than a clade. The Abyssochrysidae were tentatively considered modern zygoeuroids by Nützel.
- The ecology of the MAR Logatchev site is described by Gebruk et al. (2000), who present a fauna inventory with 11 species of gastropods, all except two (*Pseudorimula* sp. [most probably *P. midatlantica* of our list] and *Phymorhynchus moskalevi* [not listed by us from Logatchev]) not identified beyond family level.
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APPENDIX 1

List of localities with hydrothermal vents, sulphide and methane seeps from which gastropods have been reported (updated from Warén & Bouchet, 1993). The localities are listed from north to south in this order: Mid Atlantic, western Atlantic, East Pacific, and West Pacific (Figure 50). The gastropod fauna is listed by alphabetical order of genus name.

Mid-Atlantic Ridge: Menez Gwen

Position. Ca. 37°50'N, 31°31'W, 850 m.

Expedition 1. DIVA 1, May 1994, chief scientist Y. Fouquet.

Samplings. DIVA 1 PL 13 (37°50'N, 31°31'W, 844–1013 m), DIVA 1 PL 14 (37°50.46'N, 31°31.35'W, 840–870 m), DIVA 1 PL 16 (37°50.47'N, 31°31.20'W, 840 m).

Expedition 2. DIVA 2, June 1994, chief scientists D. Desbruyères & A.-M. Alayse.

Samplings. DIVA 2 PL 11, DIVA 2 PL 12, DIVA 2 PL 13, DIVA 2 PL 14, DIVA 2 PL 16, DIVA 2 PL 26 (all same position, 37°50.54'N, 31°31.30'W, 860–870 m).

Expedition 3. MARVEL, August 1997, chief scientists D. Desbruyères & A.-M. Alayse.

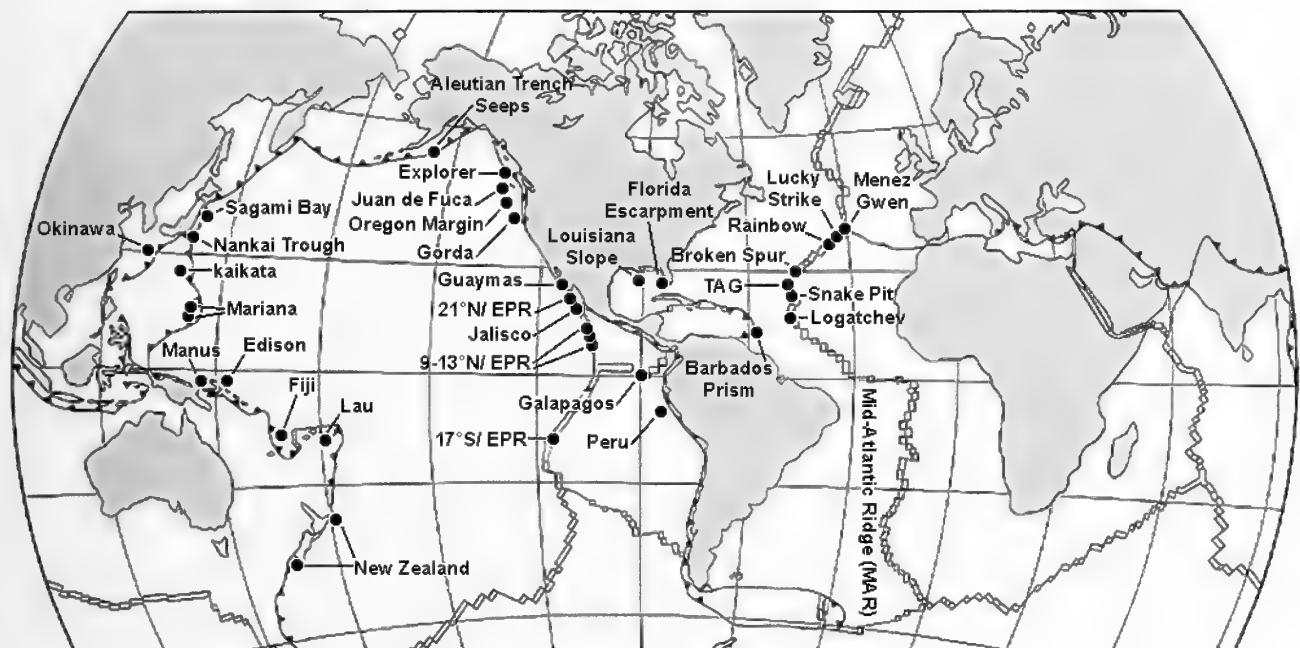


Figure 50. Localities with hydrothermal vents, sulfide and methane seeps from which gastropods have been reported. (Modified from Desbruyères & Segonzac, 1997, with permission).

Samplings. NAUTILE dives 1201 (850 m); 1202 (850 m); 1203 (850 m); 1208 (850 m); particle traps PPS 20, 24, 46, 49, 50, at the foot of a "translucid smoker" 37°50.52'N, 31°31.23'W, 845 m.

Type of locality. Area with hydrothermal vents situated at the peak of a young volcano and covering 200 m². Sulfide mounds in the area are covered by mussels. Shrimps (Alvinocarididae) common. Normal bathyal fauna is abundant at the periphery of the site.

Gastropod fauna. Warén & Bouchet herein: *Alvania stenolopha*, *Lepetodrilus atlanticus*, *Lurifax vitreus*, *Peltospira smaragdina*, *Protoliria thorvaldssoni*, *P. valvatoides*, *Shinkailepas briandi*, *Laeviphipitus desbruyeresi*, *Xylodiscula analoga* [Amphissa acuticostata (Philippi, 1844), *Anatoma* sp., *Calliostoma obesula* (Locard, 1896), *Emarginula* sp., *Neusas marshalli*, *Pedicularia* sp., *Pseudosetia azorica*, *Strobiligeria brychia* (Bouchet & Guillemot, 1988)]; species within brackets are not vent fauna, but occurred in samplings that also yielded vent species.

References. Colaco et al. (1998), Desbruyères et al. (1994a), Saldanha et al. (1996).

Mid-Atlantic Ridge: Lucky Strike

Position. Ca. 37°17'N, 32°17'W, 1620–1720 m.

Expedition 1. ALVIN dives May–June 1993, chief scientist C. Langmuir.

Samplings. ALVIN dive 2604 (37°20'N, 32°17'W, 1636 m); Dives 2605 and 2606 (37°17.55'N, 32°16.47'W, 1628 m, Statue de la Liberté); Dive 2607 (37°17.50'N, 32°16.47'W, 1628 m, Sintra site); Dive 2608 (Tour Eiffel).

Expedition 2. DIVA 1, May 1994, chief scientist Y. Fouquet.

Samplings. DIVA 1 PL 01 (37°17.49'N, 32°16.60'W, 1681–1729 m), DIVA 1 PL 03 (37°17.55'N, 32°16.47'W, 1624 m), DIVA 1 PL 04 (37°17.32'N, 32°16.51'W, 1685–1703 m), DIVA 1 PL 08 (37°17.30'N, 32°16.70'W, 1680–1728 m), DIVA 1 PL

09 (37°17.40'N, 32°16.50'W, 1622–1683 m), DIVA 1 PL 17 (37°17.32'N, 32°16.52'W, 1648–1700 m), DIVA 1 PL 18 (37°17.36'N, 32°16.65'W, 1685–1730 m), DIVA 1 PL 19 (37°17.50'N, 32°17'W, 1665–1728 m).

Expedition 3. DIVA 2, June 1994, chief scientists D. Desbruyères & A.-M. Alayse.

Samplings. DIVA 2 PL 01 (Isabel site, 37°17.36'N, 32°16.64'W, 1685 m), DIVA 2 PL 02 (Sintra site, 37°17.50'N, 32°16.47'W, 1622 m), DIVA 2 PL 03 (Isabel site), DIVA 2 PL 04 (Tour Eiffel, 37°17.32'N, 32°16.51'W, 1685 m), DIVA 2 PL 05 (Pico site), DIVA 2 PL 06 (Isabel), DIVA 2 PL 07 (Pagode site, 37°17.63'N, 32°16.95'W, 1629 m), DIVA 2 PL 08 (Tour Eiffel), DIVA 2 PL 09 (Tour Eiffel), DIVA 2 PL 10 (Tour Eiffel), DIVA 2 PL 17 (Tour Eiffel), DIVA 2 PL 19 (Pagode, Isabel), DIVA 2 PL 20 (Tour Eiffel, Isabel and Pagode), DIVA 2 PL 21 (Tour Eiffel), DIVA 2 PL 23 (Tour Eiffel and Pagode sites), DIVA 2 PL 24 (Isabel and Tour Eiffel), DIVA 2 PL 25 (Tour Eiffel and Pagode).

Expedition 4. LUSTRE Expedition, July 1996, chief scientists D. Fornari & S. Humphris.

Samplings. JASON lowerings 176, 177, 181, 183; Sintra and Tour Eiffel, as above (gastropods from C. L. Van Dover).

Expedition 5. MARVEL, August 1997, chief scientists D. Desbruyères & A.-M. Alayse.

Samplings. NAUTILE dives 1191 (Bairro Alto = Pagodes), 1192 (Bairro Alto, 1630 m), 1193 (Bairro Alto, 1585 m), 1194 (Tour Eiffel, 1685 m), 1195 (Tour Eiffel, 1685 m), 1200 (Bairro Alto, 1700 m), 1205 (Bairro Alto, 1700 m), 1206 (PP 24 site, 1643 m).

Type of locality. Hydrothermal vents around the periphery of a lava lake, dominated by *Bathymodiolus* sp. Shrimps (Alvinocarididae) common. Non-vent fishes and other fauna penetrate the area.

Gastropod fauna. Valdés & Bouchet (1998), Warén & Bouchet herein: *Alvania stenolopha*, *Dendronotus comleti*, *Laeviphipitus*

desbruyeresi, *Lepetodrilus atlanticus*, *Lirapex costellata*, *Lurifax vitreus*, *Paralepetopsis ferrugivora*, *Peltospira smaragdina*, *Phymorhynchus ovatus*, *Protolira thorvaldssoni*, *P. valvatooides*, *Pseudorimula midatlantica*, *Shinkailipes briandi*, *Sutilizona pterodon*, *Xylodiscula analoga*.

References. Desbruyères et al. (1994a), Fouquet et al. (1994), Van Dover (1995), Murton et al. (1995), Saldanha et al. (1996), Van Dover et al. (1996, 1997), Valdés & Bouchet (1998).

Mid-Atlantic Ridge: Rainbow vent field

Position. 36°13.45'N, 33°54.10'W, 2260 m.

Expedition. MARVEL, chief scientists D. Desbruyères & A.-M. Alayse, August 1997.

Samplings. NAUTILE dives 1196, 1206; particle traps (pièges à particules) PP1-10 at the base of a smoker, 36°13.81'N, 33°54.07'W, 2260 m depth.

Type of locality. Hydrothermal vents

Gastropod fauna. Warén & Bouchet herein: Conidae sp., *Lepetodrilus atlanticus*, *Protolira thorvaldssoni*, *Shinkailipes briandi*, *Xylodiscula analoga* [*Mitrella nitidulina* (Locard, 1897)]. Species within brackets are not vent fauna.

Mid-Atlantic Ridge: Broken Spur vent field

Position. Broken Spur vent field, Bogdanov site, MAR at 29°10'N, 43°10'W, 3110 m.

Expedition. BRAVEX, British-Russian Atlantic Vents Expedition 1994, chief scientist P. Tyler.

Samplings. Dive at the Bogdanov site (gastropods from P. Tyler).

Type of locality. A series of actively venting platforms and shelves on the western wall of the Eastern Valley region.

Gastropod fauna. Warén & Bouchet herein: Neritid egg capsules.

References. Murton et al. (1995), Van Dover (1995).

Mid-Atlantic Ridge: TAG vent field

Position. Kremlin site, southeastern sector of TAG hydrothermal mount, 26°08'N, 44°49'W, 3660 m.

Expedition. BRAVEX, British-Russian Atlantic Vents Expedition 1994, chief scientist P. Tyler.

Samplings. AMK 3394, Kremlin site (gastropods from P. Tyler).

Type of locality. Hydrothermal vents with *Bathymodioli*s and shrimps (Alvinocarididae).

Gastropod fauna. Sysoev & Kantor (1995), Warén & Bouchet herein: *Phymorhynchus moskalevi*.

References. Grassle (1986a), Rona et al. (1986), Galkin (1990), Fujioka & von Herzen (1994), Van Dover (1995), Humphris et al. (1995).

Mid-Atlantic Ridge: Snake Pit vent field

Position. 23°22.13'N, 44°57.13'W, 3470–3520 m.

Expedition 1. GRAVINAUT, chief scientist J. Dubois, September 1993.

Samplings. GRAVINAUT 02, Just east of “Snake Pit”; GRAVINAUT 16, “Snake Pit” site.

Expedition 2. MAR 93, Chief scientist C. L. Van Dover & A. Fiala.

Samplings. ALVIN dives 2613, 2614, 2615, 2616, 2617 (Elan site, 23°23'N, 44°56'W, 3520 m); dive 2618 (Ruches site, same

position, 3490 m); dives 2619, 2620 (Elan and Ruches sites, same position); dives 2621, 2622 (Elan site, same position).

Expedition 3. MICROSMOKE, chief scientist D. Prieur, November 1995.

Samplings. PL 07, Elan site; PL 08, Ruches site; PL 12, Ruches site, 3480 m; PL 14, Elan site, suction sample; PL 16, Ruches site, in a trap; PL 17, Elan site, 3510 m.

Type of locality. Hydrothermal vents with rich populations of mobile fauna, especially shrimps; actinians, *Bathymodioli*s and *Vesicomyia*.

Gastropod fauna. McLean (1992), Warén & Bouchet (1993) and herein: *Gymnobela* sp. B, *Lepetodrilus atlanticus*, *Lirapex* n. sp., *Peltospira smaragdina*, *Protolira valvatooides*, *P. thorvaldssoni*, *Pseudorimula midatlantica*, *Phymorhynchus carinatus*, *Phymorhynchus moskalevi*, *Phymorhynchus ovatus*, *Shinkailipes briandi*, *Sutilizona pterodon*.

References. Mevel et al. (1989), Segonzac (1992), Van Dover (1995).

Mid-Atlantic Ridge: Logatchev vent field

Position. 14°45'N, 44°59'W, 3040 m.

Expedition. MICROSMOKE, November/December 1995, chief scientist D. Prieur.

Samplings. PL 20, Irina site, 14°45.10'N, 44°48.60'W, 3005 m; PL 21, Irina site.

Type of locality. Hydrothermal vents with *Bathymodioli*s and shrimps (Alvinocarididae).

Gastropod fauna. Warén & Bouchet herein: *Peltospira smaragdina*, *Phymorhynchus carinatus*, *Phymorhynchus ovatus*, *Pseudorimula midatlantica*, *Shinkailipes briandi*.

References. Van Dover (1995), Gebruk et al. (1997).

Gulf of Mexico, Louisiana slope

Position. Bush Hill seep, 27°46.91'N, 91°30.34'W, 540–580 m.

Expedition. Chief scientist R.S. Carney.

Samplings. Johnson Sealink dive 3129, 15 Sept. 1991 (gastropods from R.S. Carney).

Type of locality. Methane seep.

Gastropod fauna. Listed by Warén & Bouchet (1993): *Bathynierita naticoidea*, *Cancellaria rosewateri*, *Cantrainea macroclani*, *Cataegis meroglypta*, *Provanna sculpta*, [*Eosipho canetae*, *Gaza fischeri*, *Gymnobela extensa*, *Hyalorisia galea*]. Species within brackets may not be strictly seep fauna.

References. Carney (1994).

Florida Escarpment

Position. West of southern Florida, 26°02'N, 84°55'W, 3270 m.

Type of locality. Sulfide rich seeps.

Gastropod fauna. *Fucaria* sp., *Paralepetopsis floridensis*, *Provanna admetooides*, neogastropods 2 spp.

Barbados Prism

Position. North Barbados, ca. 13°49'N, 57°39'W, 4940 m.

Expedition 1. BARESNAUT, chief scientists X. Le Pichon and J.P. Foucher.

Samplings. PL 94, 13°49'N, 57°39'W, 4935 m.

Expedition 2. MANON, February/March 1992, chief scientists X. Le Pichon and S. Lallemand.

Samplings. MANON 06, 13°47.05'N, 57°32.40'W, 4940 m.

Type of locality. Cold seeps; mud volcanoes surrounded by chemosynthetically active fauna.

Gastropod fauna. Warén & Bouchet herein. *Phymorhynchus* aff. *alberti*.

References. Le Pichon et al. (1990), Olu et al. (1997).

End of Barbados Prism

Position. West of Tobago, ca. 10°20'N, 1700–2000 m (Ore-noque) - 11°14'N, 1135–1236 m (El Pilar Sector).

Expedition. DIAPISUB, December 1992/January 1993, chief scientist J.C. Faugères.

Samplings. DIAPISUB 05-2, 10°20.09'N, 58°53.97'W, 1754 m; DIAPISUB 10, 1969 m; DIAPISUB 10-4, 10°19.97'N, 58°37.30'W, 1947 m, in mud; DIAPISUB 15-2, 15/8, 11°13.97'N, 59°29.92'W, 1135 m; DIAPISUB 15-4, 1135 m; DIAPISUB 16-3, 11°13.82'N, 59°21.82'W, 1236 m.

Type of locality. Cold seeps in a subduction zone (domes, mud volcanoes, and diapiric ridges), with mussels, vesicomyids and Vestimentifera.

Gastropod fauna. Warén & Bouchet herein: *Bathynerita naticoidea*, *Cataegis meroglypta*, *Phymorhynchus* aff. *alberti*, *Trophon* spp.

References. Jollivet et al. (1990), Olu et al. (1996b).

Aleutian Trench Seeps

Position. Shumagin site: 54°18'N, 157°12'W, 4800 m; Edge site: 57°27'N, 147°59'W, 4960 m.

Expedition 1. Sonne Cruise 110/1b, chief scientist E. Suess.

Samplings. Sta. 23, ROPOS (Remote Operated Platform for Ocean Science) #344, Edge site, 57°26.9'N, 147°00'W, 4947–4919 m; TVG (TV monitored grab) 24, Edge site, 57°27.631'N, 148°00.013'W, 4890 m; TVGKG (TV monitored 0.25 m² corer) 40, Shumagin site, 54°18.17'N, 157°11.82'W, 4808 m; TVG 43, Shumagin site, 54°18.196'N, 157°11.936'W, 4810 m (gastropods from H. Sahling).

Expedition 2. Sonne Cruise 110/2, chief scientist E. Suess.

Samplings. TVG 48, Shumagin site, 54°18.064'N, 157°11.895'W, 4877 m; TVGKG 49, Shumagin site, 54°18.056'N, 157°12.107'W, 4809 m; TVG 63, Edge site, 57°27.326'N, 148°00.275'W, 4774 m (gastropods from H. Sahling).

Type of locality. Sulfide/methane seeps at a subduction zone with *Calyptogena phaseoliformis*, *Acharax* cf. *johsoni*, Vestimentifera and Pogonophora. Fauna (and seepage ?) more concentrated at Edge site; diffuse at Shumagin site.

Gastropod fauna. Sahling (1997) and Warén & Bouchet herein: *Bayerius arnoldi*, *Bruceiella athlia*, *Hyalogyrina umbellifera*, *Provanna* sp. 2, *Retiskenea diploura*, *Sahlingia xandaros*. In addition, the following species were identified by McLean (unpublished) from material collected by Sahling: *Admete* sp., *Micromytilus* sp. nov., *Naticidae* sp., *Oenopota* sp.

References. Suess (1994, 1997); Lutz et al. (1996); Orange et al. (1996); Suess & Bohrmann (1997), Sahling (1997).

Juan de Fuca Ridge: Explorer Ridge

Position. Magic Mountain, Steve 4 Vent (14b), 49°45.53'N, 130°15.50'W, 1762 m.

Expedition. CANRIDGE III Expedition, July 1997, chief scientist S. Scott.

Samplings. ROPOS #284, Steve 4 Vent, 27 June 1994 (from V. Tunnicliffe).

Type of locality. Hydrothermal vents with vestimentifera, gastropods, alvinellids, and ampharetids.

Gastropod fauna. Listed by Warén & Bouchet (1993) and

herein: *Clypeosectus curvus*, *Depressigryra globulus*, *Lepetodrilus fucensis*, *Provanna variabilis*, *Speculator cariosus*, *Temnocincis euripes*.

References. Johnson (1993), Tunnicliffe et al. (1986), Tunnicliffe (1988).

Juan de Fuca Ridge: Middle Valley

Position. Off Vancouver Island, Canada, 48°25.8'N, 128°40.9'W, 2423 m.

Expedition.

Samplings. ROPOS 149, HHFA, Club Clam, 2416 m, 1992-04-07 (gastropods from V. Tunnicliffe). ALVIN dive 3146, 48°27.34'N, 128°42.57'W, 2410 m, 1997-10-06 (gastropods from J. Voight).

Type of locality. Hydrothermal vents.

Gastropod fauna. Listed by Warén & Bouchet (1993) and herein: *Clypeosectus curvus*, *Depressigryra globulus*, *Fucaria striata*, *Hyalogyrina globularis*, *Lepetodrilus corrugatus*, *L. fucensis*, *Provanna variabilis*, *Buccinum (viridum?)*.

References. Tunnicliffe (1991).

Juan de Fuca Ridge: Endeavour Segment

Position. Off Vancouver Island, Canada, ca. 47°57'N, 129°06'W, 2200–2400 m.

Expedition 1. High Rise Expedition 1995, chief scientist C.L. Van Dover.

Samplings. Advanced Tehtered Vehicle 50-1, sample 270, High Rise Vent Field, Fairy Castle edifice, 47°58.13'N, 129°05.26'W, 2200 m.

Expedition 2. BIOROPOS Expedition, chief scientist S.K. Juniper.

Samplings. ROPOS #278, Fissure at Main Field, 47°56.9'N, 129°06.9'W, 2202 m, 12 June 1994 (gastropods from V. Tunnicliffe).

Expedition 3. REVEL-ROPOS Cruise, August 1996, chief scientists S.K. Juniper, C.R. Fisher & J. Delaney.

Samplings. ROPOS HYS 351, ROPOS HYS 364, Clam Bed Vent Field, 47°57.780'N, 129°05.493'W, 2200–2250 m (gastropods from J. Voight).

Expedition 4. Not named, chief scientist J. Delaney.

Samplings. ALVIN dive 2409, 47°57'N, 129°06'W, 2192 m, Main Field, Grotto vent (gastropods from V. Tunnicliffe).

Type of locality. Hydrothermal vents.

Gastropod fauna. Listed by Warén & Bouchet (1993) and herein: *Buccinum (viridum?)*, *Clypeosectus curvus*, *Depressigryra globulus*, *Hyalogyrina globularis*, *Lepetodrilus fucensis*, *Melanodrymia brightae*, *Phymorhynchus* sp., *Provanna variabilis*, *Sutilizone tunnicliffae*, *Temnocincis euripes*.

References. Delaney et al. (1992), Johnson (1993), Juniper et al. (1996).

Juan de Fuca Ridge: CoAxial Segment

Position. Beard Chimney Source site, 46°09.3'N, 129°48.4'W, 2060 m.

Expedition. CoAxial Response, chief scientist J. Delaney.

Samplings. Grab sample from Beard Chimney Source site (gastropods from V. Tunnicliffe and C. Van Dover).

Type of locality. Hydrothermal vent.

Gastropod fauna. Warén & Bouchet herein: *Adeuomphalus trochanter*.

References. Johnson (1993), Embley et al. (1995).

Juan de Fuca Ridge: Axial Seamount

Position. Off Oregon, 45°56'N, 130°01'W, 1500–1600 m.

Samplings. ROPOS station R406, Ashes vent field, worm grab, 45°56.01'N, 130°00.87'W, 1543 m (gastropods from J. Voight).

Type of locality. Hydrothermal vents.

Gastropod fauna. Listed by Warén & Bouchet (1993), McLean & Geiger (1998) and herein: *Clypeosectus curvus*, *Cornisepta verenae*, *Depressigrya globulus*, *Lacunoides vitreus*, *Lepetodrilus fucensis*, *Provanna laevis*, *P. variabilis*, *Pyropelta musaica*, *Tlemnocinclus euripes*.

References. Tunnicliffe et al. (1985), Canadian American Seamount Expedition (1985), ASHES Expedition (1986), Tunnicliffe (1988).

Oregon Margin: 45°N

Position. 250 km west of Oregon, 44°40'N, 125°06'W, 500–800 m.

Expedition 1. Sonne Cruise 109/1, chief scientist E. Suess.

Samplings. TVG 36/1, 44°40.494'N, 125°07.268'W, 681 m; TVG 43/1, 44°40.195'N, 125°06.538'W, 609 m (gastropods from H. Sahling).

Expedition 2. Sonne Cruise 109/2-3, chief scientist E. Suess.

Samplings. TVG 109, 44°40.170'N, 125°05.796'W, 598 m, gray-green sediment with H₂S; TVG 110, 44°40.1'N, 125°05.8'W, 602 m, carbonate blocks; TVG 115, 44°40.293'N, 125°06.296'W, 616 m, from calcareous blocks; TVG 115, 44°40.293'N, 125°06.296'W, 618 m, gray-green sediment with H₂S; TVG 121, 44°40.2'N, 125°06.6'W, 622 m, gray green sediment with *Calyptogena* (gastropods from H. Sahling).

Expedition 3. Sonne Cruise 110/1a, chief scientist E. Suess.

Samplings. ROPOS #339, 44°40.3'N, 125°06.5'W, 635–632 m, sample tray 4/5; ROPOS #339, 44°40.3'N, 125°06.5'W, 635–632 m, Pete Vent Field; ROPOS #341, 44°40.14'N, 125°05.8'W, 600 m, suction sample 1; TVG 11, 44°40.134'N, 125°06.503'N, 524 m; TVG 18, 44°34.235'N, 125°08.191'W, 785 m (gastropods from H. Sahling).

Expedition 4. Juan de Fuca Cruise, July 1994, chief scientist R. Lutz.

Samplings. ALVIN dive 2796, 44°40.53'N, 125°07.10'W, 675 m, 16 July 1994 (gastropods from V. Tunnicliffe).

Type of locality. Sulfide and methane seeps at a subduction zone, with *Calyptogena* spp. and *Solemya* sp.

Gastropod fauna. Warén & Bouchet herein: (*Hyalogyrina* sp., too poor to be identified SMF 311989), *Provanna laevis*, *P. lomana*, *P. variabilis*, *Pyropelta corymba*, *Retiskenea* cf. *diploura*. In addition, the following species were identified by McLean (unpublished) from material collected by Sahling: *Boreotrophon* n. sp. (Muricidae), *Colus aphelus* (Dall, 1890), *C. halidonus* Dall, 1919, *Fusitriton oregonensis* (Redfield, 1846), *Margarites* n. sp., *Neptunea amianta* (Dall, 1890), *N. lyrata* (Gmelin, 1791), and *Pyramidellidae* gen. sp. indet.

References. Suess et al. (1985, 1996), Herzig et al. (1997), Suess & Bohrmann (1997).

Juan de Fuca Ridge, Southern Part

Position. 44°39'–44°57'N, 130°13'–130°22'W, 2200–2280 m.

Samplings. ALVIN dive 2078, Megaplume South, 1988-08-06 (gastropods from V. Tunnicliffe).

Type of locality. Hydrothermal vent.

Gastropod fauna. Listed by Warén & Bouchet (1993): *Depressigrya globulus*, *Lepetodrilus fucensis*, *Tlemnocinclus euripes*.

Gorda Ridge

Position. Off northern California, 41°00'N, 127°29'W, 3271 m.

Type of locality. Hydrothermal vents.

Gastropod fauna. Listed by Warén & Bouchet (1993): *Amphiplica gordensis*, *Depressigrya globulus*, *Lepetodrilus fucensis*, *Melanodrymia* sp., *Neolepetopsis gordensis*, *Provanna variabilis*.

Guaymas Basin

Position. Central Gulf of California, ca. 27°01'N, 111°24'W. 2020–2033 m.

Expedition. GUAYNAUT, November 1991, chief scientist A.-M. Alayse.

Samplings. PL 07 (27°00.53'N, 111°24.49'W); PL 08 (27°00.47'N, 111°24.55'W); PL 13 (27°00'N, 111°24'W); PL 15 (27°00.94'N, 111°24.50'W); PL 16 (27°00.95'N, 111°24.54'W); PL 17 (27°00.93'N, 111°24.63'W); PL 18 (27°00.93'N, 111°24.65'W).

Type of locality. Warm seeps with methane and hydrocarbons, penetrating thick layers of sediment and hydrothermal vents; vestimentifera, vesicomyids, alvinellids.

Gastropod fauna. Listed by Warén & Bouchet (1993): *Eulimella lomana*, *Hyalogyrina grasslei*, *Lepetodrilus guaymasensis*, *Provanna goniata*, *P. laevis*, *Pyropelta corymba*.

References. Unpublished report of GUAYNAUT, Grassle 1986b.

East Pacific Rise (EPR), 21°N

Position. Off southern tip of Baja California, 20°51'N, 109°04'W, 2600 m.

Type of locality. Hydrothermal vents.

Gastropod fauna. Listed by Warén & Bouchet (1993): *Bathymargarites symplector*, *Clypeosectus delectus*, *Cyathermia naticoides*, *Echinopelta fistulosa*, *Eulepetopsis vitrea*, *Gorgoleptis emarginatus*, *Lepetodrilus cristatus*, *L. elevatus*, *L. ovalis*, *L. pusillus*, *Lirapex granularis*, *L. humata*, *Melanodrymia aurantiaca*, *Neolepetopsis verruca*, *Neomphalus frettnerae*, *Nodopelta heminoda*, *Pachydermia laevis*, *Peltospira operculata*, *Phymorhynchus* sp., *Planorbidella planispira*, *Provanna ios*, *P. muricata*, *Rhynchopelta concentrica*, *Sinezona* sp., *Solutigra reticulata*, *Temnozaga parilis*.

References. Desbruyères (1998).

Remarks: A nearby locality is Green Seamount, 20°49'N, 109°17'W, 1990 m, from where *Neolepetopsis occulta* has been reported from an inactive sulfide chimney (Warén & Bouchet 1993).

Mid America Trench, Jalisco Block Seeps, at 20°N

Position. 20°N, 106°W, 3800 m.

Expedition. NAUTIMATE, chief scientists B. Mercier de Lépinay & F. Michaud, February 1994.

Samplings. NAUTIMATE PL 10, 18°22'N, 104°23'W, 3000–3300 m; NAUTIMATE PL 16, 20°01.79'N, 106°17.33'W, 3795 m; NAUTIMATE PL 18, 20°05'N, 106°18'W, 3662 m.

Type of locality. Cold seeps at the accretion zone off the Jalisco Block.

Gastropod fauna. Warén & Bouchet herein: *Bathybela papyracea*, *Bayerius* sp., *Neolepetopsis* sp., *Pleurotomella* sp., *Provanna* sp. 3, *Pyropelta* cf. *musaica*.

References. Unpublished expedition report.

East Pacific Rise (EPR), 13°N

Position. Ca. 12°49'N, 103°56.5'W, 2630 m.

Expedition 1. HERO 91, chief scientist D. Desbruyères, October 1991.

Samplings. PL 02 (Parigo, Genesis, Totem sites); PL 04 (La Chainette, 12°50.5'N, 103°57.03'W, 2600 m); PL 05 (Genesis, Totem); PL 10 (Totem, Genesis); PL 11 (Genesis); PL 12 (Genesis, Julie); PL 13 (Elsa); PL 14 (Elsa); PL 16 (Elsa, Julie); PL 17 (Elsa); PL 18 (Elsa); PL 19 (Elsa); PL 20 (Elsa); PL 21 (Elsa); PL 22 (Elsa); PL 23 (Elsa); PL 24 (Elsa); PL 25 (Caldera, 10 km south of main locality, 12°42.65'N, 103°54.65'W, 2563 m); PL 26 (Elsa); PL 27 (Totem, Genesis, Pogosud). For detailed positions of sites not given here, see Warén & Bouchet (1993).

Expedition 2. HERO 92, April 1992, chief scientist J. Chidress.

Samplings. ALVIN dives 2512 (Julie, Genesis, Parigo); 2514 (Genesis, Elsa); 2516 (Elsa, Genesis); 2517 (Elsa, Genesis); 2519 (Totem & Julie); 2520 (Parigo, Elsa, Genesis, Pogosud); 2521 (Parigo, Elsa); 2522 (Parigo, Pogosud & Genesis); 2523 (Elsa, Genesis); 2524 (Parigo, Gensis, Elsa); 2525 (Julie, Parigo, Genesis); 2526 (Julie, Parigo, Genesis); 2527 (Genesis, Elsa); 2528 (Totem, Genesis, Elsa); 2531 (Genesis); 2532 (Genesis). For detailed positions of sites not given here, see Warén & Bouchet (1993).

Type of locality. Hydrothermal vents with Vestimentifera, *Bathymodiolus*, vesicomyids, alvinellids.

Gastropod fauna. Listed by Warén & Bouchet (1993) and herein: *Bathymargarites symplector*, *Clypeolectus delectus*, *Ctenopelta porifera*, *Cyathermia naticoides*, *Echinopelta fistulosa*, *Eulepetopsis vitrea*, *Gorgoleptis emarginatus*, *G. spiralis*, *Gymnobela* sp. A., *Hirtopelta hirta*, *Lepetodrilus cristatus*, *L. elevatus*, *L. ovalis*, *L. pustulosus*, *Melanodrymia aurantiaca*, *M. "rustcovered,"* *M. galeronae*, *Moelleriopsis* sp., *Neolepetopsis densata*, *Neomphalus frettterae*, *Nodopelta heminoda*, *N. rigueae*, *N. subnoda*, *Pachydermia laevis*, *Peltospira delicata*, *P. lamellifera*, *P. operculata*, *Phymorhynchus major*, *Planorbidella planispira*, *Provanna ios*, *Rhynchopelta concentrica*, *Solutigra reticulata*, *Sutilizona theca*.

References. Fustec et al. (1987), Desbruyères (1995, 1998), Jollivet (1993).

Remarks: Other, nearby localities are "Volcano 5", 12°58.0'N, 103°26.0'W, 1160 m and "Volcano 6," 12°44.0'N, 103°33.0'W, 1775 m, from where *Clathrosepta depressa* and *Cornisepta levinae*, respectively have been described (McLean & Geiger, 1998).

East Pacific Rise (EPR), 12°N

Position. Southwest off Mexico, 11°46'N, 103°47'W, 2725 m.

Type of locality. Inactive sulfide chimney without megafaunal vent species.

Gastropod fauna. Listed by Warén & Bouchet (1993): *Neolepetopsis densata*, *Sutilizona theca*.

East Pacific Rise (EPR), 11°N

Position. Southwest off Mexico, 11°26'N, 103°47'W, 2600 m.

Gastropod fauna. Listed by Warén & Bouchet (1993): *Eulepetopsis vitrea*, *Lepetodrilus tevnianus*.

East Pacific Rise (EPR), 09°50'N

Position. 09°50'N, 104°17'W, 2505 m.

Expedition. HERO 91, October 1991, chief scientist D. Desbruyères.

Samplings. PL 06 (Worm Barbecue site, 09°50.20'N, 104°17.40'W, 2505 m); PL 07 (Brasoucade site, just south of PL 06, 09°50.09'N, 104°17.43'W, 2517 m); PL 08 (Hole to Hell site, 09°50.30'N, 104°17.50'W, 2520 m); PL 09 (Worm Barbecue site).

Type of locality. Hydrothermal vents with Vestimentifera, *Bathymodiolus*, vesicomyids, alvinellids.

Gastropod fauna. Mullineaux et al. (1996), Warén & Bouchet herein: *Bathymargarites symplector*, *Clypeolectus delectus*, *Cyathermia naticoides*, *Eulepetopsis vitrea*, *Gorgoleptis* sp., *Laviphitus* sp., *Lepetodrilus elevatus*, *Lepetodrilus ovalis*, *Lirapex granularis*, *Melanodrymia* spp., *Neomphalus frettterae*, *Pachydermia laevis*, *Peltospira delicata*, *Peltospira operculata*, *Phymorhynchus major*, *Rhynchopelta concentrica*.

References. Chevaldonné et al. (1995), Desbruyères (1998).

Galapagos Rift

Position. 00°48'N, 86°08'W, 2500–2700 m.

Type of locality. Hydrothermal vents.

Gastropod fauna. Listed by Warén & Bouchet (1993): *Clypeolectus delectus*, *Eulepetopsis vitrea*, *Gorgoleptis patulus*, *Lacunoides exquisitus*, *Lepetodrilus cristatus*, *L. elevatus*, *L. pusillus*, *Melanodrymia* sp., *Neomphalus frettterae*, *Nepotilla* sp., *Phymorhynchus* sp., *Provanna ios*, *P. muricata*.

East Pacific Rise: Northeast of Easter Island

Position. ca. 17°S, 113°W, ca. 2600 m.

Expedition. NAUDUR, J.-M. Auzende, November/December 1995.

Samplings. NAUDUR PL 03 (Nadir site, 17°25.79'S, 113°12.33'W, 2572 m); NAUDUR PL 04 (Rehu site, 1993-12-09, 17°24.85'S, 113°12.15'W, 2578 m); NAUDUR PL 06 (Rehu site); NAUDUR PL 08 (18°25.82'S, 113°12.15'W, 2623 m); NAUDUR PL 09 (Fromveur site, 18°25.96'S, 113°23.35'W, 2622 m); NAUDUR PL 18 (Le Chat, 17°24.86'S, 113°12.07'W, 2582 m; Gwen Meur, same position; Rehu), NAUDUR PL 19, site Rehu.

Type of locality. Hydrothermal vents with Vestimentifera, *Bathymodiolus*, vesicomyids, cirripeds, actinians, alvinellids.

Gastropod fauna. Warén & Bouchet herein: *Bathymargarites symplector*, *Clypeolectus delectus*, *Eosipho auzendei*, *Eulepetopsis vitrea*, *Falsimargarita nauduri*, *Lepetodrilus elevatus*, *Lepetodrilus ovalis*, *Lepetodrilus pustulosus*, *Melanodrymia aurantiaca*, *Nodopelta subnoda*, *Pachydermia laevis*, *Planorbidella planispira*, *Peltospira delicata*, *Peltospira operculata*, *Provanna ios*, *Rhynchopelta concentrica*.

References. Geistdoerfer et al. (1994), Guinot & Segonzac (1997).

Comments. Fauna very similar to the northern parts of EPR at 09–21°N.

Peru, Off Paita

Position. 05–10°S, 81–82°W, 3000–3500 m.

Expedition. NAUTIPERC, chief scientist J. Bourgois, March–April 1991.

Samplings. NAUTIPERC PL 01-4-13 (05°36.38'S, 81°42.19'W, 3542 m); NAUTIPERC PL 1-15-8 (05°42.27'S, 81°38.25'W, 2988 m); NAUTIPERC PL 02 (05°36'S, 81°41'W, 4240–3370 m); NAUTIPERC PL 18 (10°01'S, 80°07'W, 5996–5385 m).

Type of locality. Cold sulfide seeps with rich *Calyptogena* beds.

Gastropod fauna. Listed by Warén & Bouchet (1993) and herein: *Bayerius peruvianus*, *Neolepetopsis cf. gordensis*, *Tractolira sparta*.

References. Warén & Bouchet (1993), Olu et al. (1996a).

Sagami Bay

Position. 34°58'N, 139°31'E, 1130–1180 m (Okinoyama Bank); 35°00'N, 139°13'E, 1170 m (Off Hatsushima).

Type of locality. Cold seeps.

Gastropod fauna. Okutani & Fujikura (1992), Okutani et al. (1992), Okutani et al. (1993): *Bathyacmaea nipponica*, *Gymnobela sagamiana*, *Margarites shinkai*, *Phymorhynchus buccinoides*, *Provanna glabra*, *Serradonta vestimentifericola*. [Not strictly deep fauna: *Buccinum soyomaruae*, *Neptunea acutispiralis*].

References. Hashimoto et al. (1989).

Nankai Trough

Position. 33°37'N, 137°32'E, 3800–4020 m (Tenryu Canyon); 33°50'N, 137°50'E, 1900–2200 m.

Expedition. KAIKO-NANKAI, August–September 1995, leader X. Le Pichon.

Samplings. KAIKO-NANKAI PL 14, 33°49.40'N, 137°55.20'E, 2140 m.

Type of locality. Cold seeps with Vestimentifera, *Calyptogena* spp., *Solemya* sp.

Gastropod fauna. Warén & Bouchet (1993 and herein): *Bathybela* sp., *Costaria* sp. [Tenryu Canyon]; *Paralepetopsis lepi-choni*.

References. Lallement et al. (1992), Kojima & Ohta (1997).

Okinawa Back-Arc Basin: Minami-Ensei Knoll

Position. 28°24'N, 127°38'E, 700 m.

Type of locality. Hydrothermal vents with Vestimentifera, *Bathymodiolus*, and *Calyptogena*.

Gastropod fauna. Okutani & Fujikura (1990) and Okutani et al. (1993): *Bathyacmaea secunda*, *Cantrainea jamsteci*, *Lepetodrilus japonicus*, *Provanna glabra*, *Puncturella parvinobilis*. [Not strictly vent fauna: *Neptunea insularis*].

References. Hashimoto et al. (1995).

Okinawa Back-Arc Basin: Iheya Ridge

Position. 27°32.9'N, 126°58.2'E, 1350 m.

Type of locality. Hydrothermal vents.

Gastropod fauna. Okutani et al. (1993): *Bathyacmaea secunda*, *Provanna glabra*, *Lepetodrilus nux*.

Okinawa Back-Arc Basin: Izena Hole

Position. 27°16'N, 127°04.9'E, 1340 m.

Type of locality. Hydrothermal vents.

Gastropod fauna. Okutani et al. (1993): *Margarites shinkai*, *Provanna glabra*, *Puncturella rimaizenaensis*, *Lepetodrilus nux*.

Kaikata Seamount

Position. North of Iwo Jima, 26°43'N, 141°05'E, 470 m.

Type of locality. Hydrothermal vents with bythograeid crabs.

Gastropod fauna. Okutani et al. (1989), Okutani et al. (1993): *Laeviphipitus japonicus*, *Oenopota ogasawarana*, *Shinkailepas kaikatensis*.

Mariana Back-Arc Basin, Alice Springs Field

Position. North of Guam, 18°12'N, 144°43'E, 3650 m.

Type of locality. Hydrothermal vents.

Gastropod fauna. Listed by Okutani (1990), Warén & Bouchet (1993) and Hasegawa et al. (1997): *Acmaeidae* n. gen. et sp., *Alviniconcha hessleri*, *Buccinidae* sp., *Desbruyeresia marianaensis*, *Lepetodrilus* n. sp. aff. *elevatus* [= *L. schrolli*?], *Phymorhynchus* aff. *starmeri*, *Provanna nassariaeformis*, *Pseudorimula mariana*, *Shinkailepas* aff. *kaikatensis*, *Symmetromphalus regularis*, *Ventsia* aff. *tricarinata*.

Mariana Back-Arc Basin, Forecast Vent Field

Position. 13°24'N, 143°55'E, 1450 m.

Type of locality. Hydrothermal vents.

Gastropod fauna. Listed by Hasegawa et al. (1997): *Alviniconcha hessleri*, *Desbruyeresia marianaensis*, *D. aff. spinosa*, *Lepetodrilus* n. sp. aff. *elevatus* [= *L. schrolli*?], *Pachydermia* aff. *sculpta*, *Phymorhynchus* aff. *starmeri*, *Pseudorimula mariana*, *Shinkailepas* aff. *kaikatensis*, *Symmetromphalus regularis*, *Ventsia* aff. *tricarinata*.

Edison Seamount

Position. Off east coast of New Ireland, 3 miles south of Lihir Island, Edison Seamount, 03°01.185'S, 152°03.492'E, 1483 m.

Expedition. SONNE 94 Edison Expedition, chief scientist P. Herzig, on German ship *Sonne*, April 1994.

Samplings. 30-GTVA; 66-GTVA (gastropods from V. Tunnicliffe & I. Jonasson). Samplings made with a TV-monitored dredge and Russian submersible Mir-2.

Type of locality. Submarine volcano with hydrothermal vents; vesicomyids, gastropods, shrimps and actinians.

Gastropod fauna. Sysoev & Kantor (1995), Beck (1996a) and Warén & Bouchet herein: *Bathyacmaea jonassoni*, *Fucaria mystax*, *Paralepetopsis rosemariae*, *Phymorhynchus wareni*, *Provanna* sp. 1, *Puncturella solis*, *Pyropelta bohlei*.

References. Herzig et al. (1994), Beck (1996a), McInnes (1998).

Manus Back-Arc Basin: Vienna Woods

Position. Bismarck Sea, north of New Britain. Wienerwald [Vienna Woods] site: 03°09.8'S, 150°16.7'E, 2500 m.

Expedition. OLGA II, chief scientist W. Tufar, on German ship *Sonne*, May–June 1990. Samplings made with a TV-monitored dredge.

Type of locality. Hydrothermal vents.

Gastropod fauna. Beck (1991, 1992a, b, 1993), McLean & Geiger (1998): *Alviniconcha hessleri*, *Clathrosepta beckii*, *Ifremeria nautilaei*, *Lepetodrilus schrolli*, *Olgasolaris tollmanni*, *Shinkailepas tufari*, *Symmetromphalus hageni*.

References. Tufar (1990).

Manus Back-Arc Basin: PACMANUS fields

Position. Bismarck Sea, north of New Britain, ca. 03°43.6'S, 151°40.3'E.

Expedition. BIOACCESS '96 and '98 with submersible *Shinkai 2000*.

Type of locality. Hydrothermal vents.

Gastropod fauna. Hashimoto et al. (1999): *Alviniconcha* cf. *hessleri*, *Bathyacmaea jonassoni*, *Desbruyeresia melanoides*, *Eosipho desbruyeresi*, *Ifremeria nautilaei*, *Lepetodrilus schrolli*,

Lepetodrilus sp., "Margarites" sp., *Olgasolaris tollmanni*, *Phymorhynchus starmeri*, *Provanna buccinoides*, *P. nassariaeformis*, *Provanna* sp., *Shinkailepas tufari*, *Shinkailepas* sp., *Symmetromphalus hageni*.

References. Hashimoto et al. (1999).

Manus Back-Arc Basin: DESMOS Cauldron

Position. Bismarck Sea, north of New Britain, 03°41.75'S, 151°52.30'E, 2000 m.

Expedition. BIOACCESS '96 and '98 with submersible *Shinkai 2000*.

Type of locality. Hydrothermal vents.

Gastropod fauna. Hashimoto et al. (1999): *Bathyacmaea jonassoni*, *Lepetodrilus schrolli*, *Lepetodrilus* sp., "Margarites" sp., *Phymorhynchus starmeri*, *Provanna* sp., "unidentified limpet."

References. Hashimoto et al. (1999).

North Fiji Basin

Position. West of Fiji, 17°–18.8°S, 173.5°–174°W, 1955–2000 m.

Expedition 1. STARMER 2, chief scientists D. Desbruyères & S. Ohta.

Samplings. PL 10–16, PL 20–21, La Dame Blanche, 16°59.50'S, 173°55.47'W, 2000 m; PL 18–19, La Vallée des Moules, 18°50'S, 173°29'W, 2765 m.

Expedition 2. YOKOSUKA, chief scientists T. Urabe and E. Ruelan; dives with Shinkai 6500 September and October 1991.

Samplings. West of Fiji; PL 05, PL 07, PL 92, 16°59.4S, 173°54.9'E, 1966 m, (La Dame Blanche); PL 12, 18°50.59'S, 173°29.89'E, 2750 m (Sunset site).

Expedition 3. SONNE 99. Samplings made with a TV-monitored dredge, 1995.

Type of locality. White Lady and Sunset sites are hydrothermal vents with gastropods, cirripeds, Vestimentifera, *Bathymodioli*us.

Gastropod fauna. Listed by Warén & Bouchet (1993), Okutani & Ohta (1993), and Beck (1996b): 1 species of limpet, *Alviniconcha hessleri*, *Bruceiella globulus*, Buccinidae sp., *Desbruyeresia cancellata*, *D. spinosa*, *Eosipho desbruyeresi*, *Gymnobela* sp., *Ifremeria nautilae*, *Lepetodrilus schrolli* [originally as *L. elevatus*], *Leptogyra inflata*, *Olgasolaris* sp., *Pachydermia sculpta*, Patellogastropoda sp., Peltospirid sp. A, *Planorbidella depressa*, *Provanna buccinoides*, *P. segonzaci*, *Pseudorimula cf. mariana*, *Shinkailepas aff. kaikatensis*, *Symmetromphalus cf. regularis*, *Turrid* sp., unidentified Cephalaspida. *Ventsia tricarinata*.

Comments. Additional species will be reported by Beck (in press).

References. Desbruyères et al. (1994b).

Lau Basin

Position. Northwest of Tongatapu, Ride de Valufa, ca. 22°S, 177°W, 1900–1750 m.

Expedition. BIOLAU 89, chief scientist A.-M. Alayse, 1989.

Samplings. PL 01–3, PL 05, PL 07 (Hine Hina, a site with no smokers, 22°32'S, 176°43'W, 1900 m), PL 04, PL 06, 09–12 (Vai Lili, a site with smokers, 22°13'S, 176°36.5'W, 1750 m).

Type of locality. Hydrothermal vents with gastropods, cirripeds, Vestimentifera, *Bathymodioli*us.

Gastropod fauna. Listed by Warén & Bouchet (1993) and Okutani & Ohta (1993): *Alviniconcha hessleri*, *Anatoma* sp., *Bruceiella globulus*, *Cocculiniformia* sp., *Columbellidae* sp., *Desbruyeresia cancellata*, *D. melanooides*, *Eosipho desbruyeresi*, *Helicrenion reticulatum*, *Hyalogyra vitrinelloides*, *Ifremeria nautilae*, *Lepetodrilus schrolli* [originally as *L. elevatus*], *Leptogyra inflata*, *Olgasolaris* sp., *Pachydermia sculpta*, Patellogastropoda sp., Peltospirid sp. A, *Planorbidella depressa*, *Provanna buccinoides*, *P. segonzaci*, *Pseudorimula cf. mariana*, *Shinkailepas aff. kaikatensis*, *Symmetromphalus cf. regularis*, *Turrid* sp., unidentified Cephalaspida. *Ventsia tricarinata*.

Comments. Additional species will be reported by Beck (in press).

References. Desbruyères et al. (1994b).

New Zealand

Several cold seeps fields have been inferred from mollusk faunas (including *Calypogenia* and *Bathymodioli*us) collected by dredging and trawling, but so far these have not been surveyed by manned submersibles.

References. Lewis & Marshall (1996), Marshall (personal communication).

Position. Ritchie Ridge, 39°26'S, 178°24'E, 1100–1200 m.

Gastropod fauna. Limpet sp., ?*Tentaoculus* sp., *Provanna* sp. A, *Provanna* sp. B, ?*Hyalogyrina* sp., *Xylodiscula* sp., *Lurifax* sp., *Laeviphitus* sp. [as *Odostomia* sp.].

Position. Puysegur Bank, 46°58'S, 165°25'E, 960 m.

Gastropod fauna. ?*Provanna* sp. C, *Laeviphitus* sp. B.

Appendix 2

List of gastropods from hydrothermal vents and seeps, arranged alphabetically by genus name.

Species	Family/higher taxon	Type of locality	Locality
<i>Adeuomphalus trochanter</i> , sp. nov.	Vetigastropoda	vent	JdF
<i>Alvania stenolopha</i> Bouchet & Warén, 1993	Rissoidae	vent?	MAR: 37°–38°N
<i>Alviniconcha hessleri</i> Okutani, 1988	Provannidae	vent	WP: Marianas, Manus, Fiji, Lau Gorda Ridge
<i>Amphiplica gordensis</i> McLean, 1991	Cocculiniformia	vent	WP: Edison Seamount, Manus
<i>Bathyacmea jonassoni</i> Beck, 1996	Pectinodontinae	vent	WP: Fiji
<i>Bathyacmea nadinae</i> Beck, in press	Pectinodontinae	vent	Sagami Bay
<i>Bathyacmea nipponica</i> Okutani, Tsuchida & Fujikura, 1992	Pectinodontinae	seep	W: Okinawa Basin
<i>Bathyacmea secunda</i> Okutani, Fujikura & Sasaki, 1993	Pectinodontinae	vent	Jalisco Block
<i>Bathybela papyracea</i> , sp. nov.	Conidae	seep	EPR: 13°N–17°S
<i>Bathymargarites symplector</i> Warén & Bouchet 1989	Trochidae	vent	Louisiana Slope, Barbados Prism
<i>Bathynerita naticoidea</i> Clarke, 1889	Neritoidea	seep	Aleutian Trench
<i>Bayerius arnoldi</i> (Lus, 1985)	Buccinidae	seep	Off Peru
<i>Bayerius peruvianus</i> , sp. nov.	Buccinidae	seep	Jalisco Block Seeps
<i>Bayerius</i> sp.	Buccinidae	seep	Fiji, WP
<i>Bruceiella globulus</i> Warén & Bouchet, 1993	Skeneidae	vent	Aleutian Trench
<i>Bruceiella athlia</i> , sp. nov.	Skeneidae	seep	Sagami Bay
<i>Buccinum soyomaruae</i> Okutani, 1977	Buccinidae	seep?	JdF
<i>Buccinum</i> sp. (<i>viridis</i> Dall, 1890?)	Buccinidae	vent?	Louisiana Slope
<i>Cancellaria rosewateri</i> Petit, 1983	Cancellariidae	seep	WP: Okinawa Basin
<i>Cantrainea jamsteci</i> (Okutani & Fujikura, 1990)	Turbinidae	vent	Louisiana Slope
<i>Cantrainea macleani</i> Warén & Bouchet, 1993	Turbinidae	seep	Louisiana Slope
<i>Cataegis meroglypta</i> McLean & Quinn, 1987	Trochidae	seep	Louisiana Slope, Barbados Prism
<i>Clathrosepta becki</i> McLean & Geiger, 1998	Fissurellidae	vent	WP: Manus
<i>Clathrosepta depressa</i> McLean & Geiger, 1998	Fissurellidae	vent	EPR: 13°N
<i>Clypeosctetus curvus</i> McLean, 1989	Lepetodrilidae	vent	JdF
<i>Clypeosctetus delectus</i> McLean, 1989	Lepetodrilidae	vent	EPR: 21°N–17°S, Galapagos Rift
<i>Cornisepta levinae</i> McLean & Geiger, 1998	Fissurellidae	vent	EPR: 13°N
<i>Cornisepta verenae</i> McLean & Geiger, 1998	Fissurellidae	vent	JdF
<i>Ctenopelta porifera</i> Warén & Bouchet, 1993	Peltospiridae	vent	EPR: 13°N
<i>Cyathermia naticoides</i> Warén & Bouchet, 1989	Neomphalidae	vent	EPR: 21°–10°N
<i>Dendronotus comteti</i> Valdes & Bouchet, 1998	Dendronotidae	vent	MAR: 37°N
<i>Depressigyrta globulus</i> Warén & Bouchet, 1989	Peltospiridae	vent	JdF
<i>Desbruyeresia cancellata</i> Warén & Bouchet, 1993	Provannidae	vent	WP: Fiji, Lau
<i>Desbruyeresia marianaensis</i> (Okutani, 1990)	Provannidae	vent	WP: Marianas
<i>Desbruyeresia melanioides</i> Warén & Bouchet, 1993	Provannidae	vent	WP: Lau, Manus
<i>Desbruyeresia spinosa</i> Warén & Bouchet, 1993	Provannidae	vent	WP: Fiji
<i>Desbruyeresia</i> sp. aff. <i>spinosa</i>	Provannidae	vent	WP: Marianas
<i>Echinopelta fistulosa</i> McLean, 1989	Peltospiridae	vent	EPR: 21°–13°N
<i>Eosiphlo auzendei</i> , sp. nov.	Buccinidae	vent	EPR: 17°S
<i>Eosiphlo canetae</i> (Clench & Aguayo, 1944)	Buccinidae	seep	Louisiana Slope
<i>Eosiphlo desbruyeresi</i> Okutani & Ohta, 1993	Buccinidae	vent	WP: Fiji, Lau, Manus
<i>Eulepetopsis vitrea</i> McLean, 1990	Neolepetopsidae	vent	EPR: 21°N–17°S, Galapagos Rift
<i>Falsimargarita nauduri</i> , sp. nov.	Trochidae	vent	EPR: 17°S
<i>Fucaria mystax</i> , sp. nov.	Trochidae	vent	WP: Edison Seamount
<i>Fucaria striata</i> Warén & Bouchet, 1993	Trochidae	vent	JdF
<i>Fucaria</i> sp.	Trochidae	seep	Florida Escarpment
<i>Fumocapulus alaysae</i> Beck, in press	Peltospiridae	vent	WP: Fiji
<i>Gaza fischeri</i> Dall, 1889	Trochidae	seep	Louisiana Slope
<i>Gorgoleptis emarginatus</i> McLean, 1988	Lepetodrilidae	vent	EPR: 21°–13°N
<i>Gorgoleptis patulus</i> McLean, 1988	Lepetodrilidae	vent	Galapagos Rift
<i>Gorgoleptis spiralis</i> McLean, 1988	Lepetodrilidae	vent	EPR: 13°N
<i>Gymnobela extensa</i> (Dall, 1881)	Conidae	seep	Louisiana Slope
<i>Gymnobela sagamiana</i> (Okutani & Fujikura, 1992)	Conidae	seep	Sagami Bay

Appendix 2

Continued.

Species	Family/higher taxon	Type of locality	Locality
<i>Gymnobela</i> sp. A	Conidae	vent	EPR: 13°N
<i>Gymnobela</i> (?) sp. B	Conidae	vent	MAR: 23°N
<i>Helicrenion reticulatum</i> Warén & Bouchet, 1993	Trochidae	vent	WP: Lau
<i>Hirtopelta hiria</i> McLean, 1989	Peltospiridae	vent	EPR: 21°–13°N
<i>Hyalogyra vitrinelloides</i> Warén & Bouchet, 1993	Hyalogyrinidae	vent	WP: Lau
<i>Hyalogyrina globularis</i> , sp. nov.	Hyalogyrinidae	vent	JdF
<i>Hyalogyrina grasslei</i> Warén & Bouchet, 1993	Hyalogyrinidae	seep	Guaymas
<i>Hyalogyrina umbellifera</i> , sp. nov.	Hyalogyrinidae	seep	Aleutian Trench
<i>Hyalogyrina?</i> sp.	Hyalogyrinidae	seep	New Zealand
<i>Hyalarisia galea</i> (Dall, 1889)	Capulidae	seep	Louisiana Slope
<i>Ifremeria nautilei</i> Bouchet & Warén, 1991	Provannidae	vent	WP: Manus, Fiji, Lau
<i>Lacunoides exquisitus</i> Warén & Bouchet, 1989	Neomphalidae	vent	Galapagos Rift
<i>Lacunoides vitreus</i> , sp. nov.	Neomphalidae	vent	JdF
<i>Laeviphitus desbruyeresi</i> , sp. nov.	Elachisiniidae	vent	MAR
<i>Laeviphitus japonicus</i> Okutani, Fujikura & Sasaki, 1993	Elachisiniidae	vent	WP: Kaikata Seamount
<i>Laeviphitus</i> sp.	Elachisiniidae	seep	New Zealand
<i>Laeviphitus</i> sp. (veligers only)	Elachisiniidae	vent	EPR: 10°N
<i>Lepetodrilus atlanticus</i> , sp. nov.	Lepetodrilidae	vent	MAR: 38°–23°N
<i>Lepetodrilus corrugatus</i> McLean, 1993	Lepetodrilidae	vent	JdF
<i>Lepetodrilus cristatus</i> McLean, 1988	Lepetodrilidae	vent	EPR: 21°–13°N, Galapagos Rift
<i>Lepetodrilus elevatus</i> McLean, 1988	Lepetodrilidae	vent	EPR: 21°N–17°S, Galapagos Rift WP: Fiji, Lau
<i>Lepetodrilus fucensis</i> McLean, 1988	Lepetodrilidae	vent	JdF
<i>Lepetodrilus guaymasensis</i> McLean, 1988	Lepetodrilidae	seep	Guaymas Basin
<i>Lepetodrilus japonicus</i> Okutani, Fujikura & Sasaki, 1993	Lepetodrilidae	vent	WP: Okinawa Basin
<i>Lepetodrilus nux</i> (Okutani, Fujikura & Sasaki, 1993)	Lepetodrilidae	vent	WP: Okinawa Basin
<i>Lepetodrilus ovalis</i> McLean, 1988	Lepetodrilidae	vent	EPR: 21°N–17°S, Galapagos Rift
<i>Lepetodrilus pustulosus</i> McLean, 1988	Lepetodrilidae	vent	EPR: 21°N–17°S, Galapagos Rift
<i>Lepetodrilus scrollis</i> Beck, 1993	Lepetodrilidae	vent	WP: Manus
<i>Lepetodrilus tevnianus</i> McLean, 1993	Lepetodrilidae	vent	EPR: 11°N
<i>Lepetodrilus</i> sp.	Lepetodrilidae	vent	WP: Manus
<i>Leptogyra inflata</i> Warén & Bouchet, 1993	Skeneidae	vent	WP: Lau
<i>Lirapex costellata</i> , sp. nov.	Peltospiridae	vent	MAR: 37°N
<i>Lirapex granularis</i> Warén & Bouchet, 1993	Peltospiridae	vent	EPR: 21°–10°N
<i>Lirapex humata</i> Warén & Bouchet, 1989	Peltospiridae	vent	EPR: 21°N
<i>Lirapex</i> sp.	Peltospiridae	vent	MAR: 23°N
<i>Lurifax vitreus</i> , gen. et sp. nov.	Orbitestellidae	vent	MAR: 38°–36°N
<i>Lurifax</i> sp.	Orbitestellidae	seep	New Zealand
<i>Margarites shinkai</i> Okutani, Tsuchida & Fujikura, 1992	Trochidae	seep	Sagami Bay
<i>Margarites</i> sp.	Trochidae	vent	WP: Manus
<i>Melanodrymia aurantiaca</i> Hickman, 1984	Neomphalidae	vent	EPR: 21°N–17°S
<i>Melanodrymia brightae</i> Warén & Bouchet, 1993	Neomphalidae	vent	JdF
<i>Melanodrymia galeronae</i> , sp. nov.	Neomphalidae	vent	EPR: 13°N
<i>Melanodrymia</i> “rust covered”	Neomphalidae	vent	EPR: 13°N
<i>Melanodrymia</i> sp.	Neomphalidae	vent	Galapagos Rift
<i>Moelleriopsis</i> sp.	Trochidae	vent	EPR: 13°N
<i>Neolepetopsis densata</i> McLean, 1990	Neolepetopsidae	vent	EPR: 13°–12°N, Galapagos Rift
<i>Neolepetopsis gordensis</i> McLean, 1990	Neolepetopsidae	seep, vent	Gorda Ridge, Jaliso Block, Peru
<i>Neolepetopsis occulta</i> McLean, 1990	Neolepetopsidae	vent	EPR: 21°N
<i>Neolepetopsis verruca</i> McLean, 1990	Neolepetopsidae	vent	EPR: 21°N
<i>Neomphalus fretterae</i> McLean, 1981	Neomphalidae	vent	EPR: 21°–10°N, Galapagos Rift
<i>Neptunea acutispiralis</i> Okutani, Fujikura & Sasaki, 1993	Buccinidae	seep?	Sagami Bay
<i>Neptunea insularis</i> (Dall, 1895)	Buccinidae	vent?	WP: Okinawa Basin

Appendix 2

Continued.

Species	Family/higher taxon	Type of locality	Locality
<i>Neusas</i> gen nov. <i>marshalli</i> (Sykes, 1925)	Vitrinellidae	vent?	MAR: 38°N
<i>Nodopelta heminoda</i> McLean, 1989	Peltospiridae	vent	EPR: 21°–13°N
<i>Nodopelta rigneae</i> , sp. nov.	Peltospiridae	vent	EPR: 13°N
<i>Nodopelta subnoda</i> McLean, 1989	Peltospiridae	vent	EPR: 13°N–17°S
<i>Oenopota ogasawarana</i> Okutani, Fujikura & Sasaki, 1993	Conidae	vent	WP: Kaikata Seamount
<i>Olgasolaris ethmoconcha</i> Beck, in press	Neritidae	vent	Fiji: VP
<i>Olgasolaris tollmanni</i> Beck, 1992	Neritoidea	vent	WP: Manus
<i>Pachydermis laevis</i> Warén & Bouchet, 1989	Neomphalidae	vent	EPR: 21°N–17°S
<i>Pachydermia sculpta</i> Warén & Bouchet, 1993	Neomphalidae	vent	WP: Fiji, Lau
<i>Pachydermia</i> sp. aff. <i>sculpta</i>	Neomphalidae	vent	WP: Marianas
<i>Paralepetopsis ferrugivora</i> , sp. nov.	Neolepetopsidae	vent	MAR: 37°N
<i>Paralepetopsis floridensis</i> McLean, 1990	Neolepetopsidae	seep	Florida Escarpment
<i>Paralepetopsis lepichoni</i> , sp. nov.	Neolepetopsidae	seep	Nankai Trough
<i>Paralepetopsis rosemariae</i> Beck, 1996	Neolepetopsidae	vent	WP: Edison Seamount
<i>Peltospira delicata</i> McLean, 1989	Peltospiridae	vent	EPR: 13°–10°N
<i>Peltospira lamellifera</i> Warén & Bouchet, 1989	Peltospiridae	vent	EPR: 13°N
<i>Peltospira operculata</i> McLean, 1989	Peltospiridae	vent	EPR: 21°–10°N
<i>Peltospira smaragdina</i> , sp. nov.	Peltospiridae	vent	MAR: 38°–15°N
<i>Phymorhynchus</i> aff. <i>alberti</i> (Dautzenberg & Fischer, 1906)	Conidae	seep	Barbados Prism
<i>Phymorhynchus buccinoides</i> Okutani, Fujikura & Sasaki, 1993	Conidae	seep	Sagami Bay
<i>Phymorhynchus carinatus</i> , sp. nov.	Conidae	vent	MAR: 23°–15°N
<i>Phymorhynchus hyifluxi</i> Beck, 1996	Conidae	vent	WP: Fiji
<i>Phymorhynchus major</i> , sp. nov.	Conidae	vent	EPR
<i>Phymorhynchus moskalevi</i> Syssoev & Kantor, 1995	Conidae	vent	MAR: 26°–23°N
<i>Phymorhynchus ovatus</i> , sp. nov.	Conidae	vent	MAR: 37°–15°N
<i>Phymorhynchus starmeri</i> Okutani & Ohta, 1993	Conidae	vent	WP: Fiji, Manus
<i>Phymorhynchus wareni</i> Syssoev & Kantor, 1995	Conidae	vent	WP: Edison Seamount
<i>Planorbidella depressa</i> Warén & Bouchet, 1993	Neomphalidae	vent	WP: Lau
<i>Planorbidella planispira</i> (Warén & Bouchet, 1989)	Neomphalidae	vent	EPR: 21°–13°N
<i>Protolira thorvaldssoni</i> Warén, 1996	Skeneidae	vents, whale bone	MAR: 38°–36°N
<i>Protolira valvatooides</i> Warén & Bouchet, 1993	Skeneidae	vent	MAR: 38°–37°N
<i>Provanna admetoides</i> Warén & Ponder, 1991	Provannidae	seep	Florida Escarpment
<i>Provanna buccinoides</i> Warén & Bouchet, 1993	Provannidae	vent	WP: Fiji, Lau, Manus
<i>Provanna glabra</i> Okutani, Tsuchida & Fujikura, 1992	Provannidae	seep, vent	WP: Sagami Bay, Okinawa Basin
<i>Provanna goniata</i> Warén & Bouchet, 1986	Provannidae	seep	Guaymas Basin
<i>Provanna ios</i> Warén & Bouchet, 1986	Provannidae	vent	EPR: 21°N–17°S, Galapagos Rift
<i>Provanna laevis</i> Warén & Ponder, 1991	Provannidae	vent, seep	JdF, Oregon Margin, Guaymas Basin, Oregon Margin
<i>Provanna lomana</i> (Dall, 1918)	Provannidae	seep	Oregon Margin
<i>Provanna macleani</i> Warén & Bouchet, 1989	Provannidae	seep	Oregon Margin
<i>Provanna muricata</i> Warén & Bouchet, 1986	Provannidae	vent	EPR: 21°N, Galapagos Rift
<i>Provanna nassariaeformis</i> Okutani 1990	Provannidae	vent	WP: Marianas, Manus
<i>Provanna sculpta</i> Warén & Ponder, 1991	Provannidae	seep	Louisiana Slope
<i>Provanna segonzaci</i> Warén & Ponder, 1991	Provannidae	vent	WP: Lau
<i>Provanna variabilis</i> Warén & Bouchet, 1986	Provannidae	vent, seep	JdF, Gorda Ridge, Oregon Margin
<i>Provanna</i> sp. 1	Provannidae	vent	WP: Edison Seamount, Manus
<i>Provanna</i> sp. 2	Provannidae	seep	Aleutian Trench
<i>Provanna</i> sp. 3	Provannidae	vent	Jalisco Block
<i>Provanna</i> spp.	Provannidae	seep	New Zealand
<i>Pseudorimula leisei</i> Beck, in press	Lepetodrilidae	vent	WP: Fiji
<i>Pseudorimula mariana</i> McLean, 1989	Lepetodrilidae	vent	WP: Marianas
<i>Pseudorimula midatlantica</i> McLean, 1992	Lepetodrilidae	vent	MAR: 37°–15°N
<i>Puncturella parvinobilis</i> Okutani, Fujikura & Sasaki, 1993	Fissurellidae	vent	WP: Okinawa Basin

Appendix 2

Continued.

Species	Family/higher taxon	Type of locality	Locality
<i>Puncturella rimaizenaensis</i> Okutani, Fujikura & Sasaki, 1993	Fissurellidae	vent	WP: Okinawa Basin
<i>Puncturella solis</i> Beck, 1996	Fissurellidae	vent	WP: Edison Seamount
<i>Pyropelta bohlei</i> Beck, 1996	Cocculiniformia	vent	WP: Edison Seamount
<i>Pyropelta corymba</i> McLean & Haszprunar, 1987	Cocculiniformia	seep, biogenic substrates	Oregon Margin, Guaymas
<i>Pyropelta musaica</i> McLean & Haszprunar, 1987	Cocculiniformia	seep, vent, biogenic substrates	JdF, Jalisco Block
<i>Retiskenea diploura</i> , gen. et sp. nov.	Neomphalidae	seep	Aleutian Trench
<i>Retiskenea</i> sp.	Neomphalidae	seep	Oregon Margin
<i>Rhynchopelta concentrica</i> McLean, 1989	Peltospiridae	vent	EPR: 21°N–17°S
<i>Sahlingia xandaros</i> , gen. et sp. nov.	Vetigastropoda	seep	Aleutian Trench
<i>Serradonta vestimentifericola</i> Okutani, Tsuchida & Fujikura, 1992	Pectinodontinae	seep	Sagami Bay
<i>Shinkailipes briandi</i> , sp. nov.	Neritoidea	vent	MAR: 38°–15°N
<i>Shinkailipes conspira</i> Beck, in press	Neritoidea	vent	WP: Fiji
<i>Shinkailipes kaikatensis</i> Okutani, Saito & Hashimoto, 1989	Neritoidea	vent	WP: Kaikata Seamount
<i>Shinkailipes tufari</i> Beck, 1992	Neritoidea	vent	WP: Manus
<i>Shinkailipes</i> sp.	Neritoidea	vent	WP: Manus
<i>Solutigrya reticulata</i> Warén & Bouchet, 1989	Neomphalidae	vent	EPR: 21°–13°N
<i>Speculator cariosus</i> , gen. et sp. nov.	Cerithiopsidae	vent	JdF
<i>Sutilizona pterodon</i> , sp. nov.	Sutilizonidae	vent	MAR: 37°–23°N
<i>Sutilizona theca</i> McLean, 1989	Sutilizonidae	vent	EPR: 13°N
<i>Sutilizona tunnicliffae</i> , sp. nov.	Sutilizonidae	vent	JdF
<i>Symmetriapelta wareni</i> Beck, in press	Peltospiridae	vent	WP: Fiji
<i>Symmetromphalus hageni</i> Beck, 1992	Neomphalidae	vent	WP: Manus
<i>Symmetromphalus macleani</i> Beck, in press	Neomphalidae	vent	WP: Fiji
<i>Symmetromphalus regularis</i> McLean, 1990	Neomphalidae	vent	WP: Marianas
<i>Temnocrinclus euripes</i> McLean, 1989	Sutilizonidae	vent	JdF
<i>Temnozagaea parilis</i> McLean, 1989	Sutilizonidae	vent	EPR: 21°N
<i>Tentaoculus?</i> sp.	Cocculiniformia	seep	New Zealand
<i>Tractolira sparta</i> Dall, 1896	Volutidae	seep	Peru
<i>Trophon</i> sp. 1	Muricidae	seep	Barbados Prism
<i>Trophon</i> sp. 2	Muricidae	seep	Barbados Prism
<i>Ventzia tricarinata</i> Warén & Bouchet, 1993	Trochidae	vent	WP: Lau
<i>Vetulonia phalcata</i> Warén & Bouchet, 1993	Trochidae	vent	WP: Fiji
<i>Ventsia</i> sp. aff. <i>tricarinata</i>	Trochidae	vent	WP: Marianas
<i>Xylodiscula analoga</i> , sp. nov.	Xylodisculidae	vent	MAR: 37°–36°N
<i>Xylodiscula major</i> Warén & Bouchet, 1993	Xylodisculidae	vent	WP: Fiji
<i>Xylodiscula</i> sp.	Xylodisculidae	seep	New Zealand

NOTES, INFORMATION & NEWS

The Feeding Process in *Conus imperialis*

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The neogastropod *Conus imperialis* Linnaeus, 1758, has long been known to prey, evidently exclusively, on the polychaete *Eurythoe complanata* Pallas, 1766 (Family Amphelinidae), in nature (Kohn, 1959). Its prey-capturing apparatus, the radular tooth, was the first in the genus to be subjected to a detailed functional morphological analysis (Kohn et al., 1972), and congeners with morphologically similar radulae are also known or predicted to eat amphelinids (Nybakken, 1970). However, to our knowledge the actual feeding process in *C. imperialis* has never been observed. Here we describe and illustrate a case of prey capture and feeding by *C. imperialis* in the laboratory. We attempted to record similarities and differences between this and other species of *Conus*, and to observe whether feeding involves any special behavior that would make the predator less vulnerable to the unusually stiff, sharp, and urticating setae of amphelinids, commonly called "fireworms" because of their ability to penetrate human skin and cause a painful burning sensation (Eckert, 1985).

Observations

Two specimens of *Conus imperialis* (48.5 and 58.5 mm in shell length), collected by Mr. John Earle off Makua, Oahu, Hawaii in 12 m on 18 December 1999, were observed and presented with prey organisms. Only the smaller individual fed, in a tank at the Waikiki Aquarium, Honolulu, Hawaii, on 29 December 1999. The observations were made at night, when most *Conus* species are active, but under a bright fluorescent lamp to facilitate observation and video recording. The *C. imperialis* was positioned on coarse sand in the field of a digital camcorder. A specimen of *Eurythoe complanata* was placed on the sand about 2 cm in front of the shell. It began to burrow rapidly and move away from the *Conus*, but whether or not this is an escape response remains to be determined. The worm's activity moved it away from the smaller *Conus*, but toward the larger specimen, which was in another area of the same tank.

The times given below (min:sec) begin when the siphon of the smaller *Conus imperialis* was first observed to extend beyond the anterior margin of the shell. Because of the worm's burrowing and crawling behavior, we repeatedly excavated it and returned it to a position near the *Conus*.

The siphon gradually extended farther anteriad, parallel to the substrate or oriented at a downward angle (Figure 1A). It eventually (at 0:50) physically contacted the *Eurythoe*, and continued to probe. Then the proboscis sheath extended toward the worm (Figure 1B). Although in the video the proboscis is visible extending from its sheath (1:12), it was not possible to capture clearly in a single frame. The moment of injection of radular tooth and venom (1:14) was clear from the recoiling response of the worm. The *Conus* evidently released the tooth immediately from the proboscis, leaving it embedded in the worm, because a cloud of venom was observed (1:15) to rise in the water from near the point of injection (Figure 1C). This was most likely due to positive pressure from muscular contraction of the proboscis after release of the proximal end of the tooth. The effect is analogous to what would occur if a hypodermic needle were detached from the syringe while the finger continued to maintain pressure on the plunger. Only one tooth was injected into the worm. After the proboscis was withdrawn, the rhyncho daeum, also known as the proboscis sheath or "false mouth," expanded and began to engulf the now paralyzed worm. Although swallowing began immediately, the *C. imperialis* failed to consume the entire worm, which autotomized behind the wound caused by the radular tooth. This evidently occurred before the effect of the venom moved very far posteriad, as the posterior portion of the worm escaped by undulating through and then over the substrate.

We then removed the longer, posterior part of the worm, which at that point evidenced no ill effects of the venom but was bleeding at the position of autotomy, to a separate container until the *Conus* completed swallowing the anterior portion (7:25). About 15 minutes later, the *Conus* became active once more, lifting the body up on the foot and extending the siphon again. We thereupon returned the posterior end of the *Eurythoe* to the tank with the *Conus*, positioning it as before. The worm still undulated but now appeared incapable of directed movements. Upon contact, the *C. imperialis* expanded the proboscis sheath and proceeded to completely engulf the posterior portion of the worm (Figure 1D). We saw no evidence that a second radular tooth was injected.

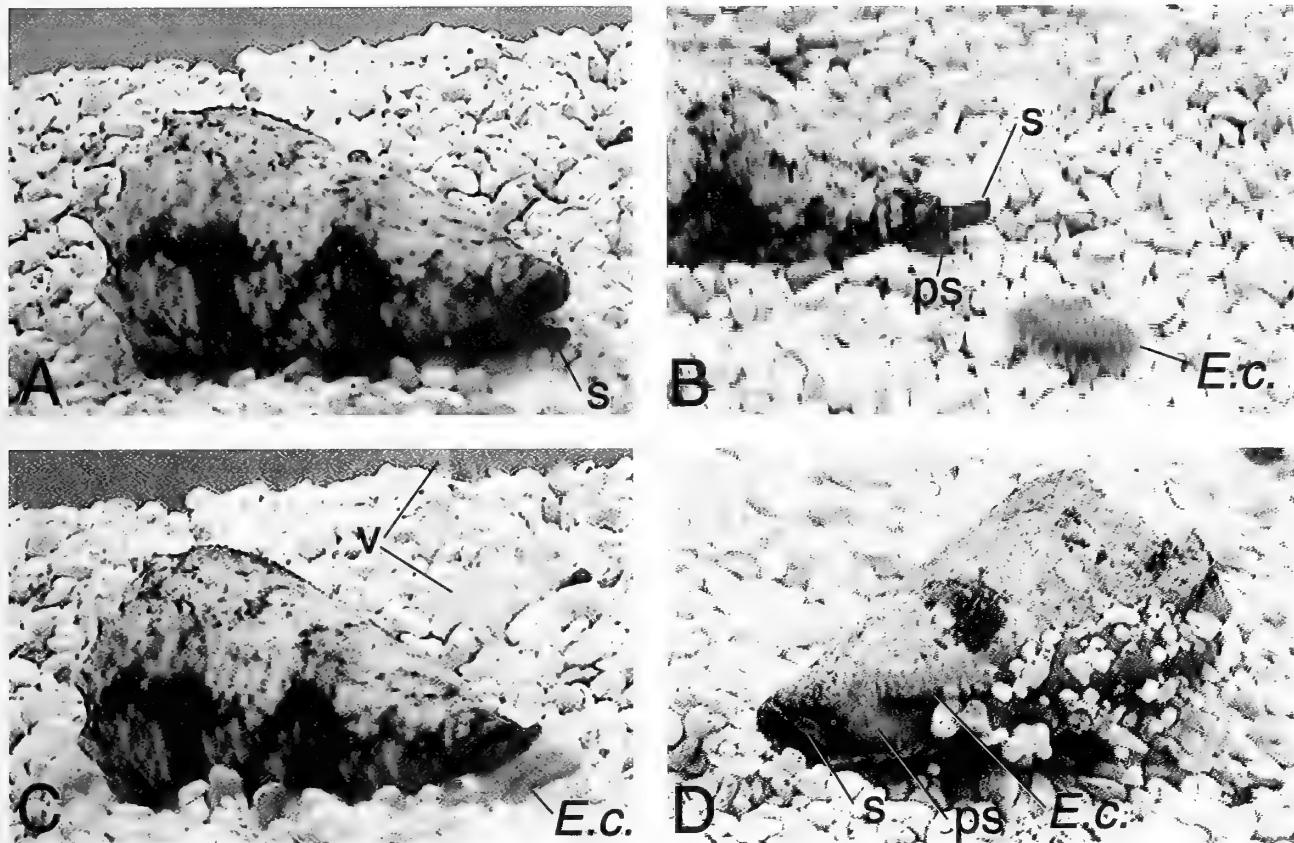


Figure 1. *Conus imperialis* (shell length 48.5 mm) from Makua, Oahu, Hawaii, feeding on the amphipod polychaete *Eurythoe complanata* Pallas, reproduced from single video frames. A. Extension of the siphon (s) along the substrate after introduction of *E. complanata* to the tank. B. Extension of the proboscis sheath or rhynchodaeum (ps), containing the proboscis, along the substrate, presumably after detection of the presence and position of *E. complanata* (E.c.). C. One second after injection of radular tooth into the prey. Release of the tooth from the proboscis (not visible) is indicated by the cloud of venom (v) rising in the water. D. The *Conus* has been manually turned over to permit observation of engulfing of the prey by the expanded proboscis sheath (ps).

Discussion and Conclusions

In observing feeding in *Conus imperialis*, for the first time to our knowledge, we attempted to detect any behavioral adaptations the predator might have to avoiding injury from the unusually long, stiff, pointed, barbed and possibly venomous setae of the amphipod polychaete *Eurythoe complanata*.

The feeding process in *Conus imperialis* differs in one important way from that of other vermivorous congeners, in that the radular tooth is released from the proboscis immediately after injection. In typical vermivorous *Conus* species, the proboscis tip retains its grip on the expanded proximal end of the tooth. The tooth and proboscis function as a harpoon and its line, with contraction of the longitudinal proboscis muscles pulling the prey into the expanded proboscis sheath (Greene & Kohn, 1989; Kohn, 1998). Release of the tooth from the proboscis after injection is typical of *Conus* species that prey on mollusks, but these typically inject two to six teeth into the same

prey, and so must release each one before loading another in the proboscis (Kohn et al., 1999).

In *Conus imperialis*, immediate release of the tooth could be a means of avoiding contact of the proboscis with the setae of *Eurythoe complanata* at the moment of stinging, when the worm is thrashing about. However, our observations detected no other distinctive behavioral features that would minimize the danger of being pricked by the setae. For example, swallowing commenced immediately as is typical in *Conus*, not after the worm died and became limp. It may be that one effect of the venom is to relax the worm's muscles sufficiently so that during swallowing (Figure 1D), the parapodia become flaccid and are deflected to a position nearly parallel to the body. This would result in the setae being swallowed from proximal to distal, that is from base to tip. Were the parapodia to be swallowed in any other orientation, their tips and forks or spurs would be more likely to penetrate and catch the skin of the predator.



Figure 2. *Conus regius* (shell length 22.6 mm) from Sorobon, Lac Bay, Bonaire, Netherlands Antilles, in the act of swallowing an amphipod polychaete. Photographed by the late Virginia Orr Maes, March 1970. The specimen is now in the Academy of Natural Sciences of Philadelphia, No. 319064.

The only other aspect of the feeding process in *Conus imperialis* not characteristic of other species in the genus is the presence in the venom of substantial amounts (5.1 nmol/mg dry venom) of serotonin (McIntosh et al., 1993). Serotonin was not detected in 13 other *Conus* species tested, although it could have been present at levels two orders of magnitude lower. It is the only neurotransmitter reported to be a conotoxin component, but whether it is functionally related to predation on amphipomids remains unknown.

Nybäkken (1970) showed that the characteristic radular tooth form of *Conus imperialis* is shared by several putatively closely related species. Two of these, the Indian Ocean *C. zonatus* Hwass in Bruguière, 1792 (Kohn & Nybakken, 1975) and the eastern Pacific *C. brunneus* Wood, 1828 (Nybäkken, 1979), also feed on *Eurythoe complanata*. They are the only *Conus* species, and to our knowledge the only predators of any sort, known to prey on amphipomid polychaetes. Nybakken (1970) also noted

that the radular tooth of the Caribbean species *C. regius* Gmelin, 1791, is also of the same form, and he predicted that it would prove to be a predator on amphipomids. To our knowledge, no one has subsequently reported on the diet of *C. regius*, but Virginia O. Maes presented the first author with a photograph of *C. regius* in the act of feeding on an amphipomid (Figure 2), thus confirming Nybakken's prediction.

We now also have independent evidence that at least some of these species are more closely related to each other than any of them is to any other congeners. DNA sequence data from one mitochondrial and one nuclear gene across more than 70 species of *Conus* indicate that the three species analyzed, *C. imperialis*, *C. regius*, and *C. brunneus*, form a distinct reasonably well supported clade (bootstrap value 70%) of predators on amphipomids (Duda & Palumbi, 1999; Duda et al., work in progress).

Acknowledgments. We thank John Earle for providing the specimens used in this study, the late Virginia Orr Maes for Figure 2, Gary Rosenberg for information on the specimen shown in that figure, and David Hurley for assistance in transferring the video images.

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BOOKS, PERIODICALS & PAMPHLETS

Bivalve Seashells of Western North America: Marine Bivalve Mollusks from Arctic Alaska to Baja California

by EUGENE V. COAN, PAUL VALENTICH SCOTT & FRANK R. BERNARD. 2000. Santa Barbara Museum of Natural History Monographs, Studies in Biodiversity: Number 2. viii + 764 pp.; ISBN 0-936494-30-1. Price (from the Santa Barbara Museum of Natural History, 2559 Puesta del Sol Road, Santa Barbara, CA 93105) \$99.00, plus \$12.00 shipping & handling in the USA.

The latest molluscan publication by the SBMNH has a long and complex history. Originally conceived in the mid-sixties as a companion to Myra Keen's *Seashells of Tropical West America*, Frank R. Bernard (1940–1989) labored for more than two decades toward the completion of this massive project. He nearly succeeded in producing a complete second draft, but when his progressing illness made continuing impossible, Gene Coan and Paul Valentich Scott stepped in. They have now, another decade since Frank's untimely death, managed to bring this immense task to completion.

This volume treats all known bivalves in the covered region, from Mexican northern Baja California to Arctic Alaska, and includes forms from the intertidal zone to abyssal depths. The hefty 4 cm (1.5 in)-thick volume (the hardcover measures 30.5 × 23 cm [12 × 9 in]) includes descriptions and illustrations for the 479 species, as well as extensive auxiliary materials such as keys, character tables, and a detailed bibliography of more than 4800 references. It is not a classic "picture book"—the reader needs to have certain familiarity with bivalves and their general classification, or needs to use the superfamily key and then browse through the pages to find the targeted taxon in one of the many interspersed black-and-white figures. As stated by the authors (p. 39), the primary goals of the book are (1) to aid in the identification of northeastern Pacific bivalves; (2) to provide access to the published information about these species, similar species, and the groups to which they are believed to belong; and (3) to pose questions that require additional study. The three authors certainly reached their goals—this book is a gem.

The opening materials reflect the complex beginnings, with separate prefaces and acknowledgments as well as an obituary (the latter by Glen S. Jamieson). The remaining introductory parts address various relevant topics, such as a brief history of eastern Pacific malacology, problems awaiting additional research, a discussion of the biogeography data of northeastern Pacific bivalves, an in-

roduction to nomenclature, a discussion of the origin of the Bivalvia, information on collecting and preserving bivalves, detailed primers on bivalve gross anatomy and shell morphology, a brief treatment of bivalve life habits, as well as technical information on the format of the book. A separate section on "Clam and Human Interaction," again authored by Glen S. Jamieson, provides interesting reading about historic and recent use of bivalves in the region.

The taxonomic part of the book begins on page 50, with a dichotomous key to superfamilies covered in this book. This leads to the 41 superfamilies in the core part of the work (pp. 60–573), comprising 66 families with 479 species. No keys are used below the level of superfamily; here, identification is greatly aided by well designed character tables. The book closes with valuable guides to bivalve literature, a reference section that presents one of the best malacological bibliographies ever published, and useful tools such as a geologic time scale and a geographic guide providing geodetic data for localities cited in the text. The appendix of image sources (listing full data for each photograph and most species drawings) will be extremely valuable for subsequent workers. A comprehensive glossary and an alphabetic index complete the book.

The species-level taxonomic work and the incredibly complete bibliography reflect the care and great attention to detail for which the authors are already known. The literature references to morphological, biological, and taxonomic works cited with each taxon make this book a fountain of information—useful far outside the stated geographic limits. It should be noted that the following taxonomic actions are included (and clearly indicated as such) in the book: Three species are described as new, with varying authorship: *Adontorhina lynnae* Valentich Scott, 2000 (Thyasiridae); *Tellina (Angulus) cadieni* Valentich Scott & Coan, 2000 (Tellinidae); *Tresus allomyax* Coan & Valentich Scott, 2000 (Mactridae). Also, subsequent designations for the type species of the genus-group taxa *Junonia* Seguenza, 1877, and *Cultellus* Conrad, 1837, are made.

I see two areas in which a future edition could further improve this work. One concerns the illustrations, consisting of original and reproduced line drawings as well as digitally produced black-and-white photographs (plus a smaller number of SEM images): The authors provide anatomical drawings to illustrate each of the nominal genera for which such material could be found in the literature. These give excellent impressions of the generalized soft-body morphology of the respective taxon, often il-

lustrating one of the discussed species, and it would be good to extend this to include the remaining taxa (which, of course, would require availability of anatomical material and production of original anatomical illustrations). More importantly, it would be better if the figures were annotated—all labeling by the original figure authors was stripped for this book. Because the images come from various sources and differ in their emphasis of certain anatomical features, comparison between the various images is sometimes difficult. The photographic images, particularly those of the outside of the shells, are of good quality. However, the inside aspects are not always optimal; the lighting could have been better; the strong shadows cast into the concave valves obfuscate much information, particularly the shape and position of muscle scars and mantle lines. In the description of Tellinidae and Macomidae, this is nicely offset by additional line drawings of both inside valves. Detailed photographs or drawings of additional shell hinges (and—now I'm getting greedy—of prodissococonchs to facilitate identification of larvae and juveniles . . .) are also on my wish list for a second edition. The generous layout of the book, with frequent white spaces, would have allowed for larger magnification of the existing illustrations—in particular, the overlapping arrangement of inside and outside valves in the photographs was not necessary and resulted in hidden detail.

The other area involves the supraspecific taxonomy that underlies this book. The Preface by EVC and PVS includes the following paragraph: "The basic text for most of the generic, family-level, and higher taxa remains chiefly as Frank had it, except where change was required for style, clarity, and format. This material has mostly not been checked against what were his chief sources, Cox et al. (1969) and Boss (1982), nor was it feasible to add information from more recently published works, such as J. G. Carter (1990a)." This admitted 10-year lag makes the book a bit of a hybrid, in which certain parts seem somewhat frozen in time, whereas others are based on original, more recent, taxonomic updates (an example is the synonymy of the venerid subfamilies Venerinae and

Chioninae). The new parts are not necessarily identified in the volume but, because of the overlap of authors, it is no surprise that there is strong congruence between this work and the taxonomic decisions in the previously published checklists by Coan & Scott (1997) and Turgeon et al. (1998).

Technically, the book is well produced, with solid binding, good-quality paper, and a remarkably low number of typographic errors and omissions (and these are mainly restricted to foreign language citations among the thousands of entries in the bibliography). Extremely helpful to the user is the nice touch of listing the respective bivalve family name prominently on the bottom of each page, making "thumbing" through the book a breeze.

The Santa Barbara Museum of Natural History advertises this as a "must have" publication for malacologists, paleontologists, archeologists, libraries, shellfishery and environmental scientists, and shell collectors," and I wholeheartedly agree. This is an instant classic, one that belongs on the reference shelf, right next to the time-honored *Seashells of Tropical West America* by Myra Keen and Tucker Abbott's *American Seashells*.

Rüdiger Bieler

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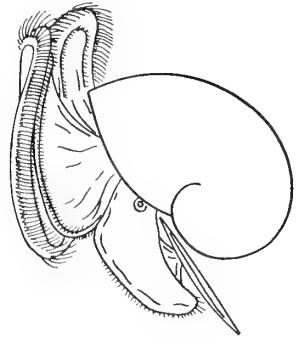
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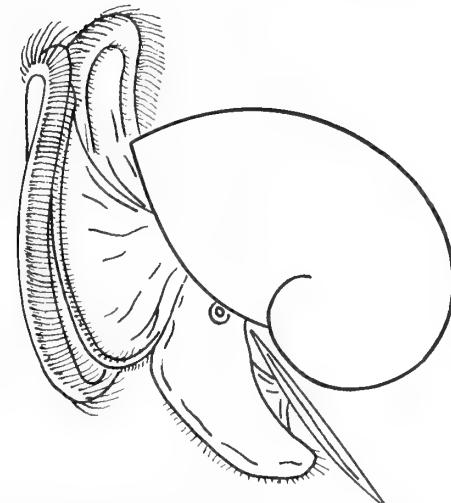


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Late Reproductive System Development in Two Cephalaspideans (Gastropoda: Opisthobranchia): *Bulla striata* Bruguière, 1792, and *Acteocina atrata* Mikkelsen & Mikkelsen, 1984

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Abstract. Development of the hermaphroditic reproductive system was investigated in two monaulic opisthobranchs *Bulla striata* Bruguière, 1792 [Bulloidea], and *Acteocina atrata* Mikkelsen & Mikkelsen, 1984 [Philinoidea], representing the two major clades of Cephalaspidea, using histological serial sectioning of growth series. The female glandular masses of the two species are similar, each possessing three major glands (albumen, mucus, membrane) presumably depositing protective layers around fertilized eggs during oviposition. These glands assume similar configurations in the two species, but each gland of *B. striata* intercepts the gonoduct separately at its base, whereas the glands of *A. atrata* have a common point of intersection. The retractile copulatory organs of the two species each include an outer penial sheath, a sperm-storing duct, and a terminal sac. The copulatory organ of *B. striata* is more complex, including a duct-within-a-duct section containing a non-glandular penial extrovert plus a coiled prostatic ejaculatory duct. Fortuitous sectioning of a specimen with its copulatory organ partially everted revealed that while this species has no permanent penial papilla, the penial extrovert everts to form the functional penis. The copulatory organ of *A. atrata* is a simple penial sheath widening into a papillose medial duct and glandular terminal sac; the presence of a penial papilla was unconfirmed, and the function of the organ remains unresolved. Ontogenetic timing in *A. atrata* is protandric, with male ducts and gonadal tissue fully developed (assuming full functionality) before the female components; *B. striata* appears to be a true simultaneous hermaphrodite, with male and female systems maturing concurrently.

INTRODUCTION

Character coding for phylogenetic analysis depends upon having sufficient data to make reasonable assumptions about homologies. In gastropods (the largest and most diverse primary clade of Mollusca), use of reproductive structures in systematic research has been problematic in this regard. This is particularly true in taxa with internal fertilization, in which a variety of structures have evolved to store reproductive products and to protect developing eggs. Ponder & Lindberg (1997:195), in their monumental phylogenetic analysis of gastropods, specifically ignored “accessory reproductive structures such as glands and sperm sacs . . . because of their doubtful homology across major groups.” To add to the confusion caused by the sheer structural diversity, gastropod reproductive systems are mosaic structures, in which two or more organogenetic components contribute to the adult system. Many of the terms used to refer to parts of the adult reproductive system are based on assumptions about their ontogenetic origins, which are not documented for most

gastropod species. Uncritical use of such terminology can mask systematically informative data.

This work is part of a larger study to investigate structural homologies within complex gastropod reproductive tracts by analyzing post-larval ontogeny in growth series of selected species. The reproductive system is indeed the only organ system whose ontogeny can be studied in post-larval individuals because it is the last system to develop, and its differentiation is largely post-metamorphic. This has in fact contributed to the lack of data on reproductive system ontogeny because embryological studies generally disregard post-metamorphic processes while morphological studies generally ignore immature stages.

Comparison of reproductive anatomy between heterobranchs and other gastropods has been particularly difficult due to (1) disparate structural names based more on location or sheer assumption than on knowledge of fine structure or function (especially regarding sperm storage sacs and the “female” glands associated with nutritive and protective layers of the egg mass); (2) different anatomical orientations in torped gastropods and “untorted” heterobranchs; and (3) separate male and female tracts in dioecious gastropods versus combined tracts in hermaphroditic heterobranchs.

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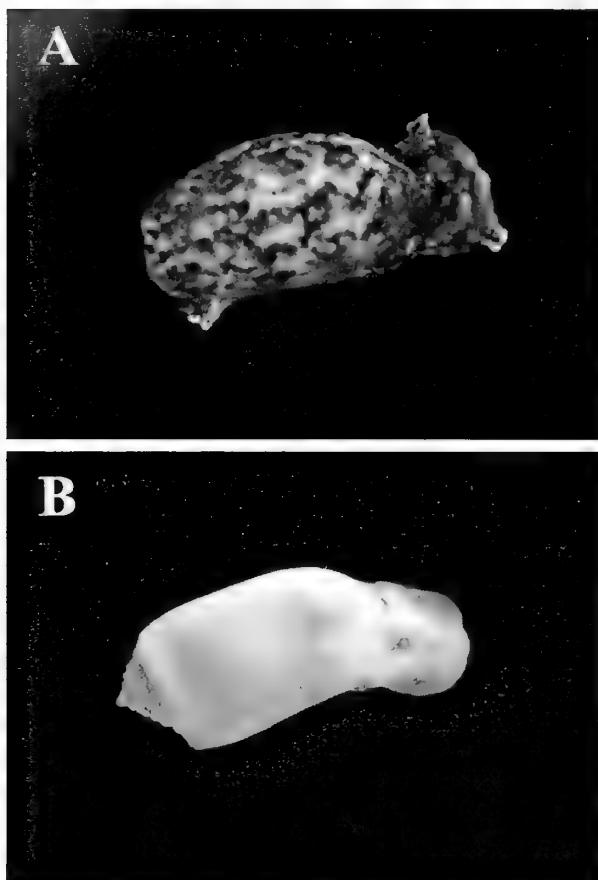


Figure 1. Living animals of species studied herein. A. *Bulla striata* [Bulloidea: Bullidae], (FK-004, 13.0-mm specimen). B. *Acteocina atrata* [Philinoidea: Acteocinidae], (PSM-842, 4.24-mm specimen).

In a recent phylogenetic analysis of Cephalaspidea (traditionally the most primitive living opisthobranchs) and other basal heterobranchs (Mikkelsen, 1996), Cephalaspidea was redefined and found to comprise two major clades at the subfamily level: Bulloidea and Philinoidea. In the latter study, characters of certain structures in the monaulic hermaphroditic reproductive tract (e.g., male “prostate” gland, female glandular mass) were not codable because “gross morphology and cellular configuration appeared to be highly variable [and] homology could not be presumed” (Mikkelsen, 1996:402). The current study focuses on one representative from each of these clades—*Bulla striata* from Bulloidea (Figure 1A), and *Acteocina atrata* from Philinoidea (Figure 1B)—with the immediate goal of comparing adult morphologies and corresponding ontogenetic patterns within Cephalaspidea, and the ultimate aim of contributing to a morphological data set including caenogastropods and members of other gastropod groups.

MATERIALS AND METHODS

Material (Table 1)

Sectioned *Bulla striata* specimens were from: (1) R/V *FLORIDAYS* station FK-163 (10 specimens sectioned, 3.4–11.3 mm; vouchers AMNH 290095), dredged in sandy mud and turtlegrass (*Thalassia testudinum* Banks ex König), with chicken liver sponge (*Chondrilla nucula* Schmidt) and *Dasycladus* green algae, 5.6 ft (1.7 m), off the Florida Bay side of Tavernier, Key Largo, Monroe County, Upper Florida Keys, 25°03'36.6"N, 80°30'0.0"W to 25°03'35.5"N, 80°30'2.2"W, 12 September 1998, P. M. Mikkelsen & R. Bieler, coll.; (2) R/V *FLORIDAYS* station FK-211 (2 juveniles sectioned, 2.5–3.2 mm; vouchers AMNH 290096), bottom sample in turtlegrass, in an unnamed bay between Shark Key and Big Coppitt Key, Florida Bay side, Monroe County, Lower Florida Keys, 24°36.38'N, 81°39.18'W, 17 April 1999, P. M. Mikkelsen & R. Bieler, coll.; (3) station PSM-767 (1 adult sectioned, 16.5 mm), sieving in shoalgrass (*Halodule wrightii* Ascherson), 40 cm depth, cove near Haulover Canal, northern Indian River Lagoon, Brevard County, central eastern Florida, 28°44'40.0'N, 80°45'5.5'W, 10 February 1981, P. S. Mikkelsen et al., coll.; (4) station PMM-931 (1 adult sectioned, 12.5 mm), sieved from sand and turtlegrass, less than 1.0 m depth, “the horseshoe” relic harbor on Florida Bay side of Spanish Harbor Keys, Monroe County, Lower Florida Keys, 24°39'19"N, 81°18'13"W, 24 January 1988, P. M. Mikkelsen & R. Bieler, coll. Additional comparative data were obtained from a sectioned copulatory organ dissected from an adult (30.2 mm) from shallow sand and seagrass, Hobe Sound, Palm Beach County, southeastern Florida, 24 March 1979, HBOM [Harbor Branch Oceanographic Museum, Ft. Pierce, Florida] 065:02023 [utilized by Mikkelsen, 1996]. The live specimen photographed of *B. striata* was from sta. FK-004, seagrass bed on the ocean side of Crawl Key, Monroe County, Florida Keys, 2 October 1994.

All sectioned *Acteocina atrata* specimens (7 specimens sectioned, 1.4–3.1 mm; vouchers AMNH 290097) were sieved from sandy mud in flats off Little Jim Island [LJI], Indian River Lagoon, Ft. Pierce, St. Lucie County, central eastern Florida, August 1989, J. Wise, coll. The live specimen photographed was from sta. PSM-842, muddy sand at the mouth of Turnbull Creek, northern extent of Indian River Lagoon, Volusia County, central eastern Florida, 30 May 1982.

All specimen sizes are expressed as shell length. All animals were fixed in Bouins’ fixative or 5% formalin, then transferred to 70–75% ethyl alcohol. All photographs show the specimens in cross-section, from a head-on perspective, so that left and right sides are reversed. Voucher specimens are deposited in the Recent mollusk collection of the Division of Invertebrate Zoology, American Museum of Natural History.

Comparative Anatomy

Data for this project were drawn from histological serial sections of whole individuals of *Bulla striata* and *Acteocina atrata*. After measurement, shells were removed by soaking intact specimens for several hours in 10% acetic acid. Dissecting pins were used to pierce the gizzard region of large specimens of *A. atrata*, to allow the acid to reach the calcified gizzard plates. This step was not necessary for *B. striata*, which has corneous (uncalcified) gizzard plates. The shell-less specimens were then passed through a dehydrating and infiltrating series, and embedded in Paraplast (Oxford Labware, St. Louis, Missouri). They were sectioned either perpendicular to the coiling axis or parallel to it, at 6–10 µm for *B. striata* and 5–8 µm for *A. atrata*. Most sections were stained in Harris' hematoxylin (Vacca, 1985) and counterstained with eosin Y (Humason, 1962)/phloxine (Vacca, 1985) (hereafter H&E). Sections of the adult *B. striata* from PMM-931 and HBOM 065:02023 were stained with Alcian-Blue/Periodic Acid/Schiff's (PAS) trichrome stain. All staining reactions are those of H&E, unless otherwise noted.

Specimens were considered "adult" when both spermatozoa and ova were observed in the gonad. The description of the hermaphroditic system follows the pathway of exiting reproductive products, i.e., from gonad to external genital opening; that of the copulatory organ follows the pathway of entering autosperm, i.e., from external to internal, or from male genital opening to terminal sac.

RESULTS

A summary of the results, indicating the relative timing of appearance and differentiation of various reproductive organs, is given in Table 1. The gross anatomy of the adult reproductive system in *Bulla striata* and *Acteocina atrata* is shown in Figures 2A, B, respectively.

Posterior Gonoduct

In this study, the term posterior gonoduct refers to the gonad (interdigitated with the digestive gland in the apical coil of the snail) and its immediate duct. The duct extends from its origin at the gonad, including the expanded and coiled ampulla (Figures 2A, B [amp]), to a sphincter located just posterior to the female glandular mass (Figures 2A, B [ring surrounding gonoduct]; called sphincter gonoductus by Lemche, 1956). In previous heterobranch literature, the posterior gonoduct has been called the coelomic gonoduct (Ghiselin, 1966; Robles, 1975) or the hermaphroditic duct (Marcus, 1957; Thompson & Bebbington, 1969; Haszprunar, 1985; Gosliner, 1994). Coelomic gonoduct (implying mesodermal origin) is not used here because there is not definitive evidence for the junction site of the ectodermal (female glandular

mass) and mesodermal (gonad) portions of the duct. Without such evidence, a more general term that does not imply a specific ontogenetic origin is preferable. Hermaphroditic duct seems imprecise for this portion alone because the entire gonoduct is hermaphroditic in the sense that both ova and sperm exit the snail via this pathway.

Bulla striata

The gonad of *Bulla striata* is similar to that of *B. gouldiana* (Pilsbry, 1893), as described by Robles (1975). As in the latter species, oogenesis occurs at the outer parts of the gonadal acini, and spermatogenesis toward the inside (Figure 3A). The gonad empties into the ampulla. The ampulla is wide and slightly coiled, and is packed with sperm in the three sectioned adults. The epithelium consists of large, irregularly shaped nonsecretory cuboidal cells, with short cilia. The ampulla extends about one-third to one-half of a shell whorl, and ends directly posterior to the female glandular mass, where there is a funnel-shaped muscular valve here called a sphincter (Figures 2A [ring surrounding gonoduct] and 4A). The sphincter could function to prevent the premature passage of sperm (as suggested by Lemche, 1956), or it could be an artifact generated by the imperfect fusion of mature mesodermal and ectodermal tissues. In each case, the end of the anterior gonoduct overlaps the end of the posterior gonoduct like a sleeve (shown in cross-section of an immature individual, Figure 4B). Just before the sphincter, the ampulla narrows considerably, and the wall becomes more muscular.

In the growth series of immature specimens examined (2.5–11.2 mm), the sphincter develops gradually, first as a weaker version of its mature morphology. Sperm and/or ova are not evident in any of these specimens. The posterior gonoduct is represented only by a narrow uncoiled duct, running straight along the columellar wall and branching into the digestive gland. The epithelium is dense and undifferentiated throughout.

Acteocina atrata

Separate male and female acini in the gonad of *Acteocina atrata* are difficult to distinguish. As Mikkelsen & Mikkelsen (1984) reported, this species has nonplanktic development, with an uncleaved egg diameter at deposition of about 150 µm. Mature ova in the gonad are very large, and can fill the entire whorl width (between the outside body and columellar walls) when viewed in cross-section (Figure 3B). They are characterized by the presence of numerous pink-staining yolk droplets and a large well-defined nucleus and nucleolus that stain pale pink and dark pink, respectively. Their large size relative to the gonoduct suggests that either the ova must distort or the gonoduct must expand to allow egg deposition.

The ampulla extends about one-half whorl. The pos-

Table 1
Material examined and ontogenetic development of the reproductive tract. [ad = adult, g = present and glandular, ju = juvenile, n = not present, — = not seen or not applicable].
p = present but nonglandular, x = present, — = not applicable.

<i>Bulla striata</i>												<i>Actaeolina atrata</i>												
Copulatory Organ	FK-	FK-	FK-	FK-	FK-	FK-	FK-	FK-	FK-	FK-	FK-	FK-	FK-	FK-										
	211	211	163	163	163	163	163	163	163	163	163	163	163	163	163	163	163	163	163	163	163	163	163	
Station no. (see text)	ju	ju	ju	ju	ju	ju	ju	ju	ju	ju	ju	ju	ju	ju										
Developmental stage	2.5	3.3	3.4	4.0	5.0	5.4	6.0	7.4	9.0	10.0	11.2	11.4	12.5	16.5	1.4	1.4	1.4	1.4	1.4	1.4	1.4	1.4	1.4	
Shell length (mm)																								
sexual maturity												female maturity												
Invagination	x	—	x	x	—	x	—	x	—	x	—	x	—	x	—	x	—	x	—	x	—	x	—	x
Double-walled duct	—	x	—	—	x	—	—	x	—	x	—	x	—	x	—	x	—	x	—	x	—	x	—	x
Adult epithelia	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Female Gland Mass																								
Gametolytic gland duct	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x?	x	x	x	x	x	x	
Gametolytic gland	n	p	n	p	p	p	p	p	p	p	p	p	p	p	p	p	—	—	g	g	g	g	g	
Albumen gland	p	p	p	p	p	p	p	p	p	p	p	p	p	p	p	p	p	p	p	p	p	p	p	
Mucus gland	p	p	p	p	p	p	p	p	p	p	p	p	p	p	p	p	p	p	p	p	p	p	p	
Membrane gland	n	p	p	p	p	p	p	p	p	p	p	p	p	p	p	p	p	p	p	p	p	p	p	
Sperm-storage pouch	x?	x	n	x	x	x	x	x	x	x	x	x	x	x	x	x	n?	—	x	x	x	x	x	
Posterior Gonoduct												male maturity												
Ampulla	—	—	—	n	n	—	n	n	n	n	n	n	n	n	n	n	x	x	x	x	x	x	x	
Spermatozoa	—	—	—	n	n	—	n	n	n	n	n	n	n	n	n	n	x	x	x	x	x	x	x	
Ova	—	—	—	n	n	—	n	n	n	n	n	n	n	n	n	n	—	—	n	n	n	x	x	

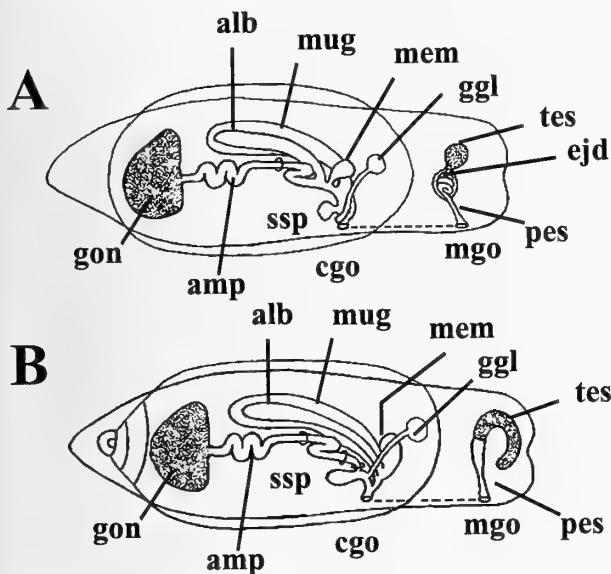


Figure 2. Diagrammatic gross reproductive anatomy in adult animals. A. *Bulla striata*. B. *Acteocina striata*. Key: alb = alumen gland; amp = ampulla; cgo = common genital opening; ejd = ejaculatory duct of copulatory organ; ggl = gametolytic gland; gon = gonad; mem = membrane gland; mgo = male genital opening; mug = mucus gland; pes = penial sheath of copulatory organ; ssp = sperm-storage pouch; tes = terminal sac of copulatory organ; ring surrounding gonoduct = sphincter.

terior portion of the ampulla is wide, and the contained sperm are oriented in an irregular swirled pattern (Figure 4C). The anterior portion of the ampulla (Figure 2B [amp]) is relatively straight, and ends in a sphincter, as in *Bulla striata*, near the posterior side of the female glandular mass. The ampullar epithelium consists of irregularly shaped cuboidal cells, similar to that in *B. striata*.

In the smallest specimen (1.4 mm), a small amount of mature sperm is visible in the gonad, but no mature ova. The ampulla in this specimen has not fully developed, but is present as a wide duct with nonciliated cuboidal epithelium. The sphincter is also not developed in the smallest specimen, but it is present in all others; no gradual development of the sphincter was noted. Mature ova are present only in the largest animals (2.7–3.1 mm).

Anterior Gonoduct

Traditional names of the glands in the female glandular mass refer to their presumed function, which is difficult to assess and seldom backed by evidence. The female glands assumed present in cephalaspideans—alumen, mucus (= nidamental), and membrane (= capsule, winding)—have been discussed by a number of authors (e.g., Lemche, 1956; Ghiselin, 1966; Thompson, 1976; Hadfield & Switzer-Dunlap, 1984). In the absence of strong evidence about what each contributes to a deposited egg mass, but in the interest of terminological stability, we

will refer to them by these conventional names. [A particularly unconventional approach was used by Rudman (1971) in describing the three female glands in *Haminoea zelandiae* (Gray, 1843)—he used “genital gland mass” for the alumen and membrane glands (evidenced from cross-sections, egg pathways, and presumed homology statements), and presented a two part—posterior and anterior “(or pallial)”—mucus gland.]

The terms traditionally applied to exosperm storage pouches—seminal receptacle (= receptaculum seminis, spermatocyst) and bursa copulatrix (= copulatory bursa)—are likewise strongly linked to their presumed function—long- or short-term storage of oriented (embedded) or unoriented sperm, respectively (Fretter & Graham, 1994). These two terms are also heavily linked to location in gastropods—the bursa copulatrix near the common genital opening, and the seminal receptacle more proximal to the gonad near a fertilization chamber. In the two taxa examined here, two pouches occur near the common genital opening. One of these is clearly the gametolytic gland (= spermatheca, ingesting gland), containing degenerating sperm and other reproductive products. The other contains oriented sperm in at least one specimen, but we hesitate to label it “seminal receptacle” because of its location well after the point at which exiting eggs would have received their protective coatings from the female glands. We therefore refer to it generically as a sperm-storage pouch.

The female glands are part of the anterior gonoduct, defined from the sphincter just posterior to the female glandular mass to the common genital opening on the animal's right side. This region is commonly referred to as the pallial gonoduct (e.g., Ghiselin, 1966; Hadfield & Switzer-Dunlap, 1984). That term is not used here because (as with the term ‘coelomic gonoduct’) the exact location of the transition point between the ectodermal (pallial) and mesodermal (coelomic) gonoduct is unconfirmed. The narrow muscular tube just inside the common genital opening (that presumably receives the copulatory organ of the mating partner) is here called the vagina, in accordance with Marcus (1957) and Gosliner (1994). The wide muscular anterior part of the gonoduct, located posterior to the vagina near the female glands and sperm sacs, is called the vestibule, in accordance with Fretter & Graham (1994).

Bulla striata

The female glandular mass is located on the floor of the pallial cavity posterior to the point where the foregut passes into the posterior body cavity. The main body of the glandular mass is complex, and in mature animals the various parts are difficult to discriminate. The major components of the glandular mass are oriented antero-posteriorly. The anterior gonoduct enters the glandular mass from the rear on the left side, then turns right and tra-

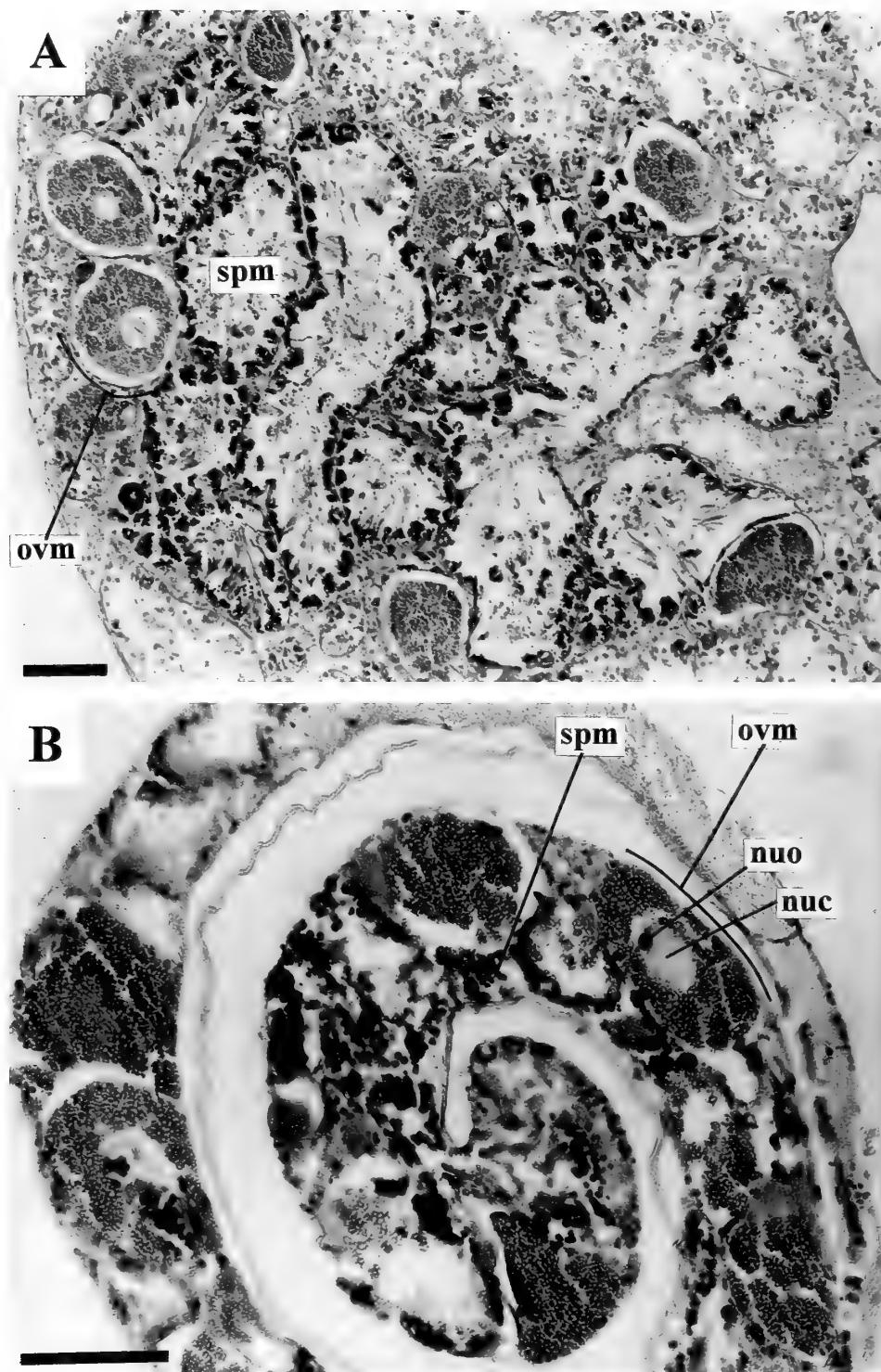


Figure 3. Cross-sections showing mature gonadal acini. A. Single acinus in *Bulla striata* (FK-163; 11.4-mm specimen). B. Posterior body coil in *Acteocina atrata* (3.2-mm specimen). Scale bars = 100 μm . Key: nuc = nucleus; nuo = nucleolus; ovm = mature ovum; spm = sperm.

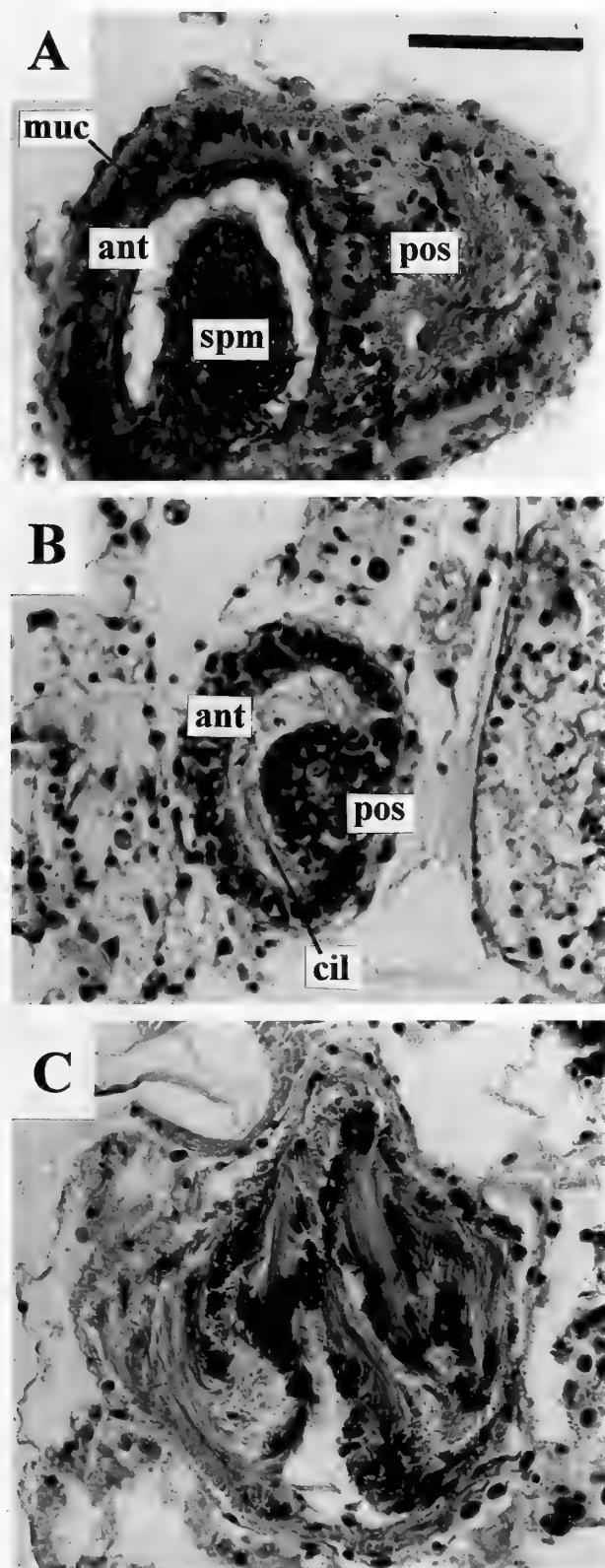


Figure 4. Portions of the posterior gonoduct. A. Tangential section of fully developed sphincter of *Bulla striata* (PSM-767;

verses within the bases of the glands and into the vestibule.

From the sphincter, the anterior gonoduct becomes narrow and ciliated, with mucoidal cells interspersed in the epithelium. This duct runs anteriorly nearly to the wall of the pallial cavity, then turns posteriorly along the glandular mass for a long distance. It loops and passes back anteriorly on the left side of the gland. Its epithelium becomes entirely mucoidal. The albumen gland lumen opens into the duct close to the posterior part of the loop. This loop of duct is equivalent to the post-ampullar duct of Robles (1975).

The three large glands of the female glandular mass have different staining reactions. The two largest components of the mature mass are the albumen and mucus glands. The albumen gland (Figure 2A [alb]) is the first one encountered by exiting eggs in the gonoduct. It is very long, almost equal in length to the visceral mass, but shorter than the mucus gland partially surrounding it. The albumen gland is many cell layers in thickness. Its cells stain pale purplish red, primarily from the eosin and phloxine stains. In the specimen stained with PAS, the cells are bright magenta in color. This gland is a diverticulum, emptying into the gonoduct, rather than comprising or surrounding the gonoduct, as depicted by Marcus (1957:fig. 5). The lumen of the gland is narrow and densely ciliated (Figures 5A, B).

The mucus gland (Figure 2A [mug]) is longer than the albumen gland, and is composed of larger cells (Figure 5B [mug]). It wraps around the albumen gland over most of its length, but its wide base is to the right of the albumen gland. As a result, its lumen is distal to that of the albumen gland where it contacts the main channel of the gonoduct (Figure 2A [mug]). The cells of the gland stain pale purplish white, primarily with hematoxylin. In the specimen stained with PAS, the cells stain pale purple, with some regions turquoise (suggestive of mucus). The lumen is ciliated; one wall has a pale red-staining columnar epithelium with central nuclei, the other side is stained like the rest of the gland. Farther posteriorly, close to the albumen gland, there is a region with smaller cells that stains more strongly with hematoxylin, and appears pale purple in sections. The anteriormost region of the mucus gland, near the common genital opening, has distinctly smaller cells.

The lumen of the anterior gonoduct at this point becomes very complex and is difficult to follow in sections. Part of the duct opens into a thick-walled gland on the

16.5-mm specimen). B. Cross-section of immature sphincter of *B. striata* (FK-163; 11.2-mm specimen). C. Sperm (in swirled pattern) in ampulla of *Acteocina atrata* (2.7-mm specimen). Scale bars = 50 μ m. Key: ant = anterior gonoduct; cil = cilia; muc = mucus cell; pos = posterior gonoduct; spm = sperm.

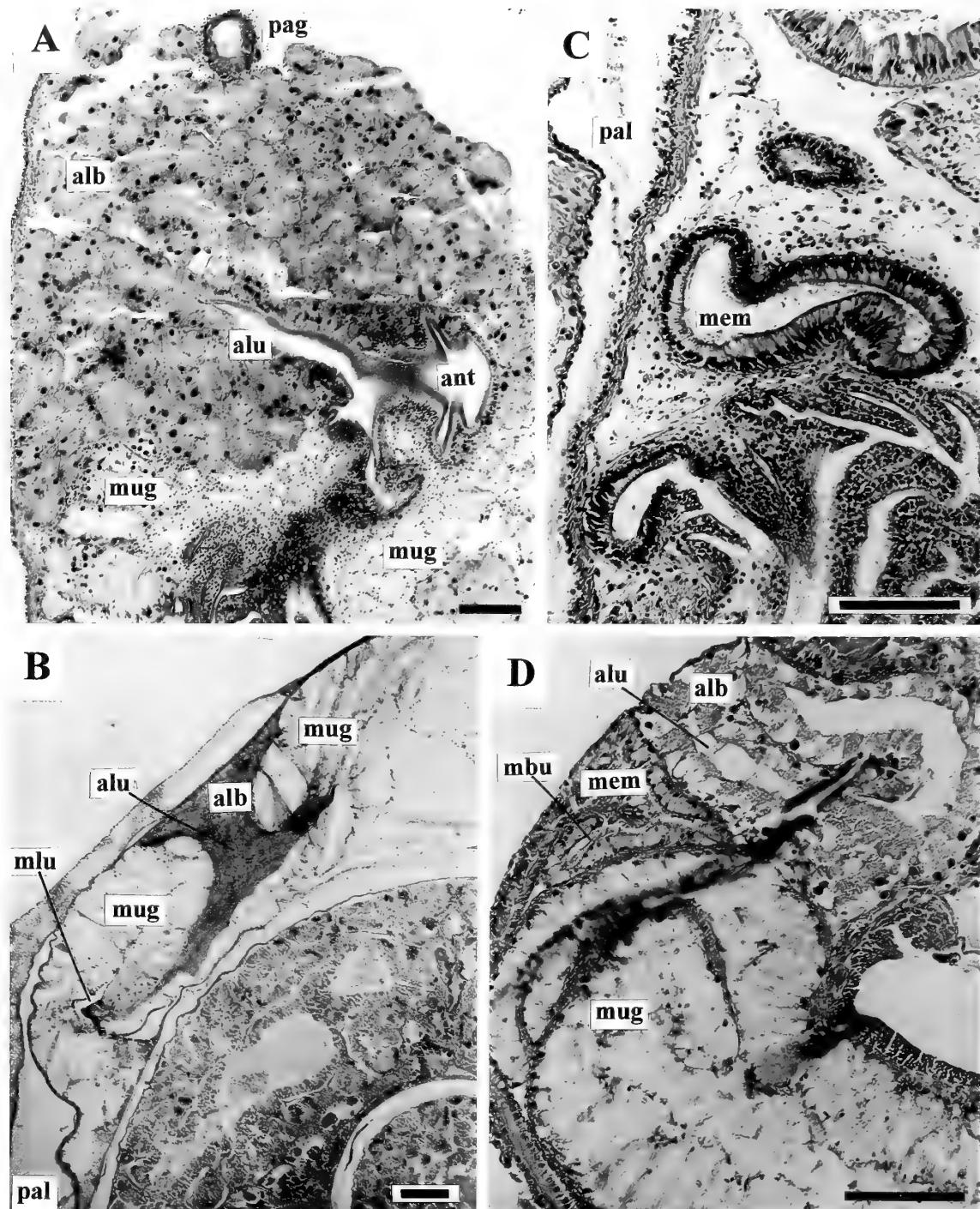


Figure 5. Female glandular mass. A. Cross-section of albumen gland in *Bulla striata*, at its junction with the gonoduct (PSM-767, 16.5-mm specimen). B. Cross-section of posterior ends of albumen and mucus glands in *B. striata*, showing the former nested in the latter (PSM-767, 16.5-mm specimen). C. Cross-section of membrane gland in immature *B. striata* (PSM-767, 16.5-mm specimen). D. Cross-section of female glandular mass in *Acteocina atrata* (2.7-mm specimen). Scale bars = 100 μm (A, C, D); 200 μm (B). Key: alb = albumen gland; alu = lumen of albumen gland; ant = anterior gonoduct; cil = cilia; mbu = lumen of membrane gland; mem = membrane gland; mlu = lumen of mucus gland; muc = mucus cell; mug = mucus gland; pag = posterior end of anterior gonoduct; pal = pallial cavity; pos = posterior gonoduct; spm = sperm.

anterior left side of the glandular mass, which is S-shaped in cross-section. Gosliner (1979) referred to a small gland at this position in *Acteocina canaliculata* (Say, 1826) as the membrane gland, and we use this term here. The epithelium of this gland has tall, pale-purple-staining columnar cells, with long cilia and basal nuclei (Figure 5C [mem]). There are no subepithelial glandular tissues associated with it. The gland is a diverticulum, but its body lies extended toward the pallial cavity instead of toward the posterior alongside the albumen/mucus glands. At the blind end of the gland, the right wall becomes nonglandular, and has a columnar ciliated epithelium.

In the same region, the anterior gonoduct enters the dense network of narrow folds or tubules that makes up the anteriormost part of the glandular mass, and turns right toward the common genital opening. The walls in this region are thin. The epithelium is cuboidal, with a few mucus cells; the presence of cilia could not be confirmed. The main part of the anterior gonoduct in this region also has a ciliated cuboidal epithelium. The sperm-storage pouch and the gametolytic gland (see below) open here, nearby each other on the posterior side of the glandular mass.

The sperm-storage pouch (Figure 2A [ssp]) is a small diverticulum. Its walls consist of narrow columnar cells with central nuclei. In the largest specimen (16.5 mm), the lumen contains mucus and a few oriented sperm with their heads embedded in the epithelial wall (Figure 6A [spm]). The outside wall is muscular.

The duct of the gametolytic gland passes anteriorly from the anterior gonoduct into the pallial/pericardial wall, alongside a posterior extension of the pericardium (which ends along the body wall near the glandular mass, slightly to its left). The gland is muscular in mature animals, with a tall, dense epithelium. The terminal sac of the gametolytic gland (Figures 2A, 6B [ggl]) is located adjacent to the pericardium in the pallial cavity roof. In mature specimens, this is spherical with thin walls. The epithelium is composed of tall columnar cells with central nuclei. Its lumen in the largest specimen (16.5 mm) is filled with yellow- and pink-staining material, but no obvious sperm, as is present in the other adult specimens (11.4 and 12.5 mm).

Just before the common genital opening, the anterior gonoduct branches into two vestibular chambers (Figure 7A [vec]). One chamber leads to the vagina and common genital opening. The other is a blind chamber next to the body wall that communicates with the right side of the mucus gland, which is located adjacent to the anterior side of the gonoduct. Both of these chambers are muscular. The epithelia are similar, and consist of dense ciliated columnar cells with central nuclei. Some regions along the vestibular wall have yellow-staining particles in the cells.

One adult (11.4 mm) has a large amount of sperm in the anterior gonoduct. In this animal, the sperm is found

in the gametolytic gland and in the vestibule, between the vagina and the densely folded region on the anterior left side (Figure 7B [spm]). None is present in the sperm-storage pouch (Figure 7B [ssp]). The gonoduct wall is markedly distended by the large amount of sperm.

In one of the small specimens (3.4 mm; Figure 8A), the glandular mass is partially differentiated, and the posterior gonoduct is present. The glandular mass in this animal consists of small sacs representing the albumen and mucus glands. The gametolytic gland duct and the coiled section of duct anterior to the sphincter are also present. The base of the glandular mass near the common genital opening is a simple oval chamber, which splits posteriorly into the mucus gland to the left of the opening and the albumen gland to the right (Figure 8A [mug, alb]). Both glands are U-shaped in cross-section at the base. The albumen gland becomes round in cross-section posterior to where the two glands diverge, and becomes nested within the 'U' of the mucus gland (Figure 8B, shown in a slightly larger specimen). The epithelia are undifferentiated and densely nucleated. The posterior gonoduct, as it extends away from the glandular mass, has a less dense epithelium.

In small specimens, the gametolytic gland is a small darkly nucleated hollow sphere at the end of its duct. In progressively larger specimens, the lumen enlarges and bulges into the pericardial lumen. The epithelia of the gametolytic gland and its duct consist of low cuboidal cells, and the wall is nonmuscular. In the smallest animals, both the main part of the glandular mass and the gametolytic gland duct open into the pallial cavity at the same place, and they are only narrowly connected to each other. Thus it appears that they might develop as independent invaginations from the same site on the pallial wall, but this was not positively confirmed.

The anterior gonoduct differentiates relatively early. In the 5.0-mm specimen, the common genital opening is located a short distance to the right of the main body of the glandular mass (instead of immediately anterior to it), indicating that the vestibule has started to develop. The future glandular regions posterior to the vagina have thicker, cuboidal epithelia. The walls of the vagina and glandular mass are still nonciliated. In the 7.4-mm specimen, the anterior wall of the glandular mass has a few folds, and the vestibular and vaginal walls are ciliated. The first glandular tissues in the gonoduct appear in the membrane gland, as shown in Figure 5C.

As the anterior gonoduct develops, it changes shape. This change is particularly apparent in the position of the common genital opening. In the smallest animals, the differentiating glandular mass and the gametolytic gland duct open at the same place (Figure 9A), along the pallial wall adjacent to the anterior tip of the digestive gland. Continuing development of the glandular mass effectively carries the gametolytic gland duct away from the body

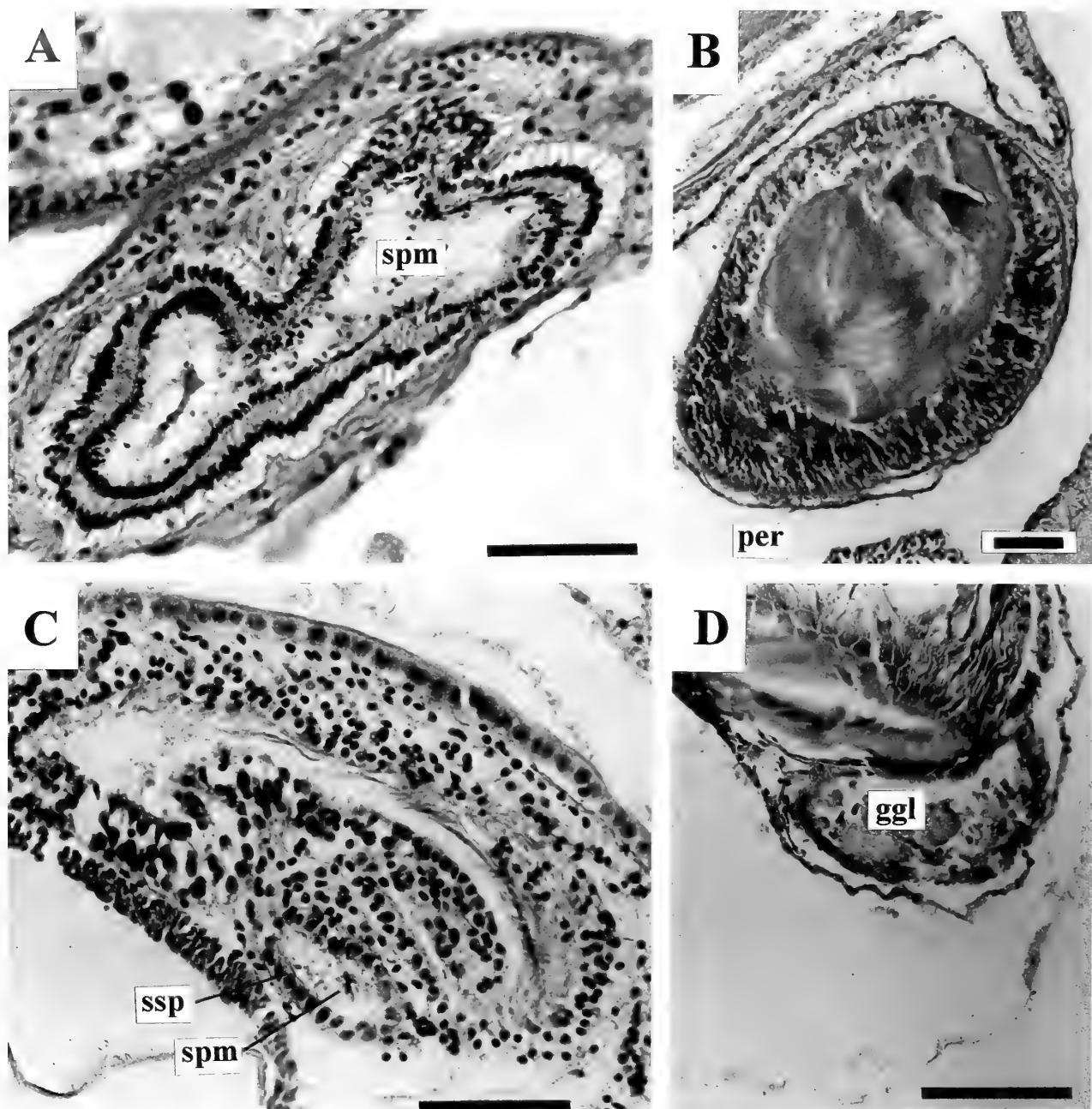


Figure 6. Sperm-storage pouches and gametolytic glands. A. Tangential section of sperm-storage pouch containing sperm in *Bulla striata* (PSM-767; 16.5-mm specimen). B. Tangential section of gametolytic gland in *B. striata* (FK-163; 11.4-mm specimen). C. Cross-section of gonoduct showing sperm-storage pouch containing sperm in immature *Acteocina atrata* (2.0-mm specimen). D. Tangential section of gametolytic gland in *A. atrata* (3.1-mm specimen). Scale bars = 50 µm (A, C); 100 µm (B, D). Key: ggl = gametolytic gland; per = pericardium; spm = sperm; ssp = sperm-storage pouch.

wall, and in larger animals it opens into the ventral side of the gonoduct near the sperm-storage pouch (Figure 8C). The common genital opening is shifted progressively to the right from its original location, as described in the previous paragraph (Figures 9B, C). As a result, the common genital opening and gametolytic gland duct in ad-

vanced juveniles and adults are some distance apart, in different regions of the gonoduct. The mucus gland also changes shape with ontogeny. The base is narrow in the smallest animals, but it broadens as the vestibule develops, and it remains connected to a large portion of the vestibule roof.

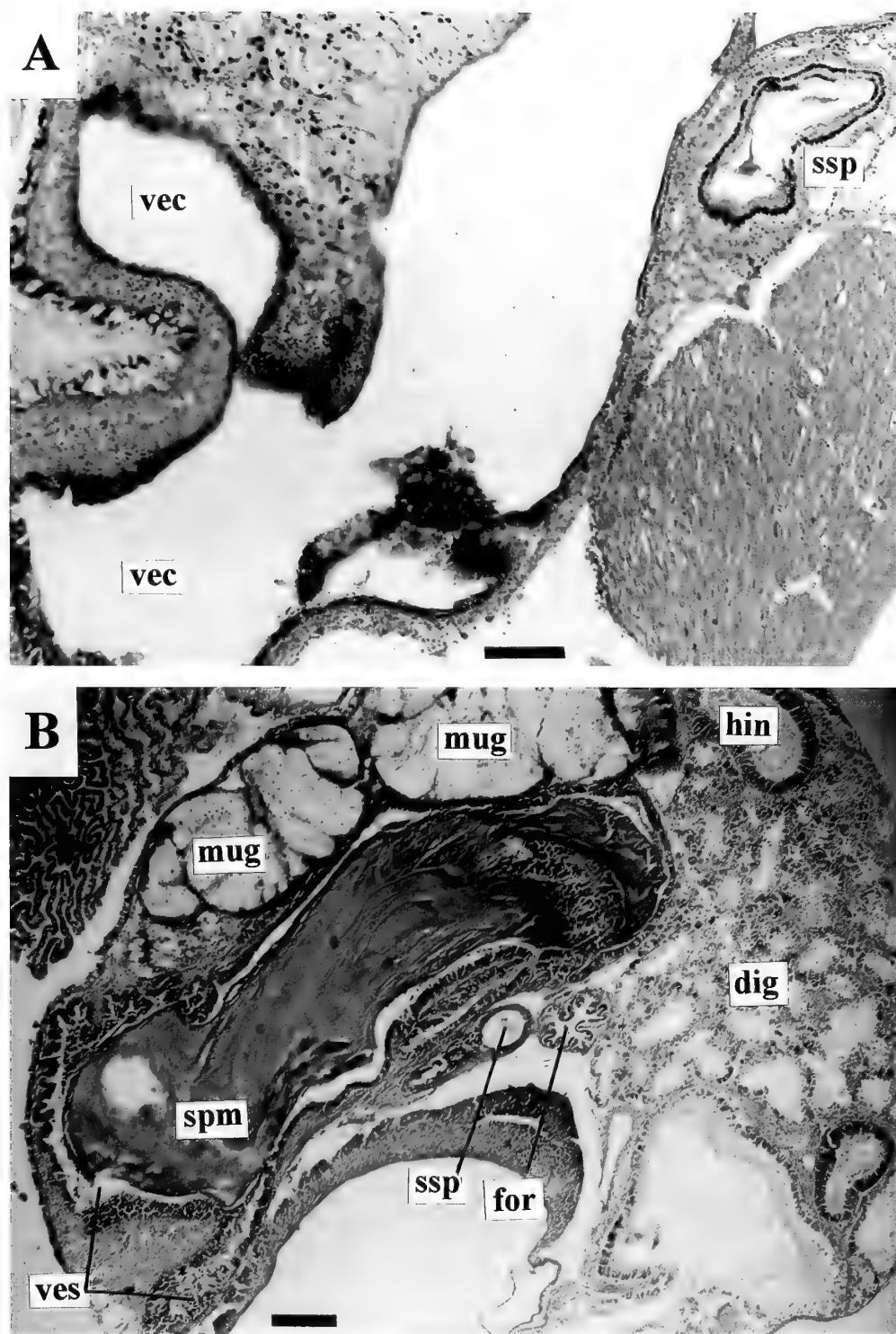


Figure 7. Vestibule in *Bulla striata*. A. Tangential section of vestibular chambers (PSM-767; 16.5-mm specimen). B. Sperm in anterior gonoduct and vestibule (FK-163, 11.4-mm specimen). Scale bars = 100 μm (A); 200 μm (B). Key: dig = digestive gland; for = foregut; hin = hindgut; mug = mucus gland; ssp = sperm-storage pouch; vec = vestibular chambers; ves = vestibule.

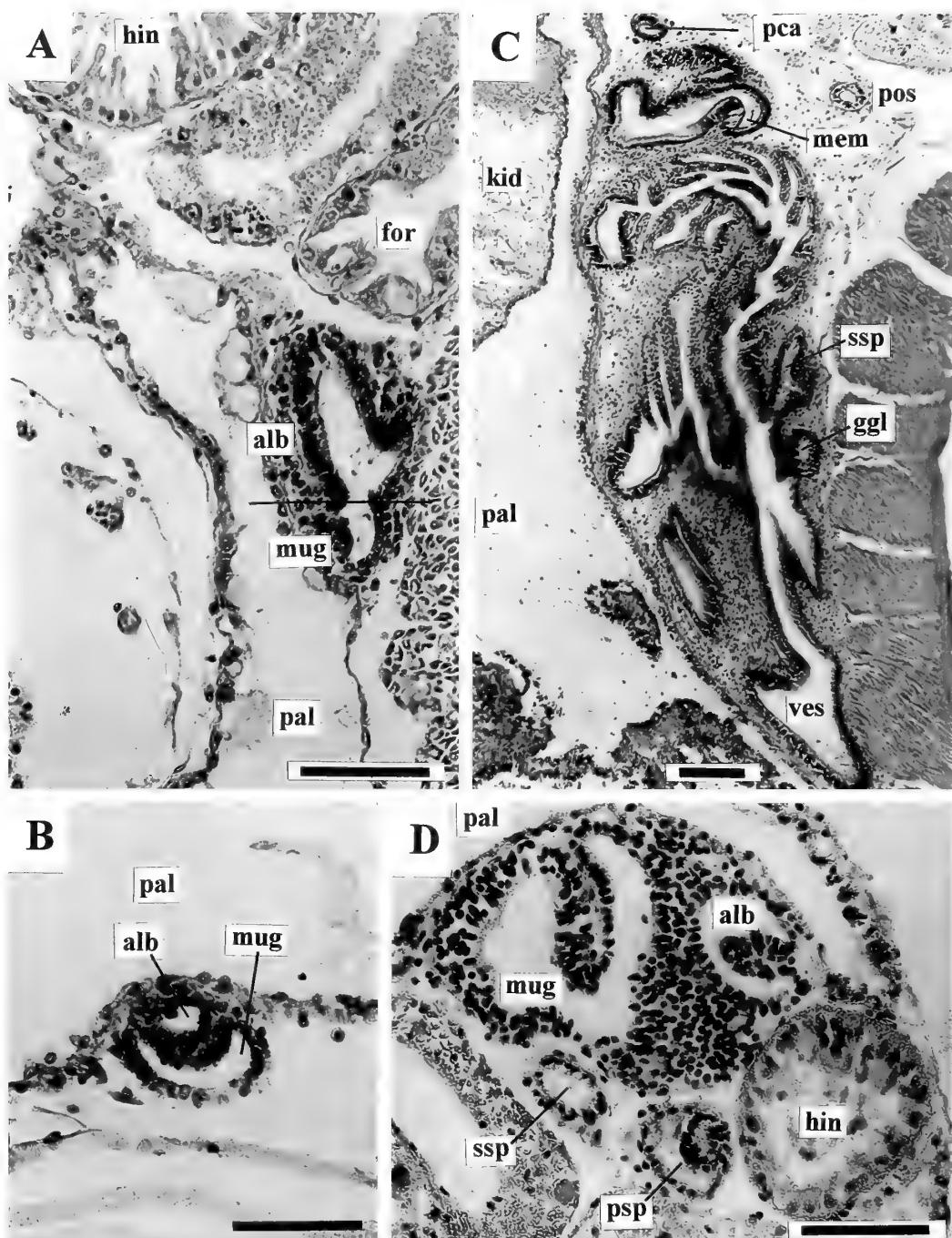


Figure 8. Developing anterior gonoduct. A. Cross-section of the base of the mucus and albumen glands in juvenile *Bulla striata* (FK-163; 3.4-mm specimen). B. Cross-section of albumen and mucus glands in juvenile *B. striata* (FK-163; 4.0-mm specimen). C. Overview of developing anterior gonoduct in *B. striata* (FK-163; 11.2-mm specimen). D. Posterior region of anterior gonoduct of *Acteocina atrata* (1.7-mm specimen). Scale bars = 50 μm (A, B, D); 100 μm (C). Key: alb = albumen gland; for = foregut; hin = hindgut; kid = kidney; mem = membrane gland; mug = mucus gland; pal = pallial cavity; pca = posterior coil of anterior gonoduct; pos = posterior gonoduct; psp = posterior sphincter; ssp = sperm-storage pouch; ves = vestibule.

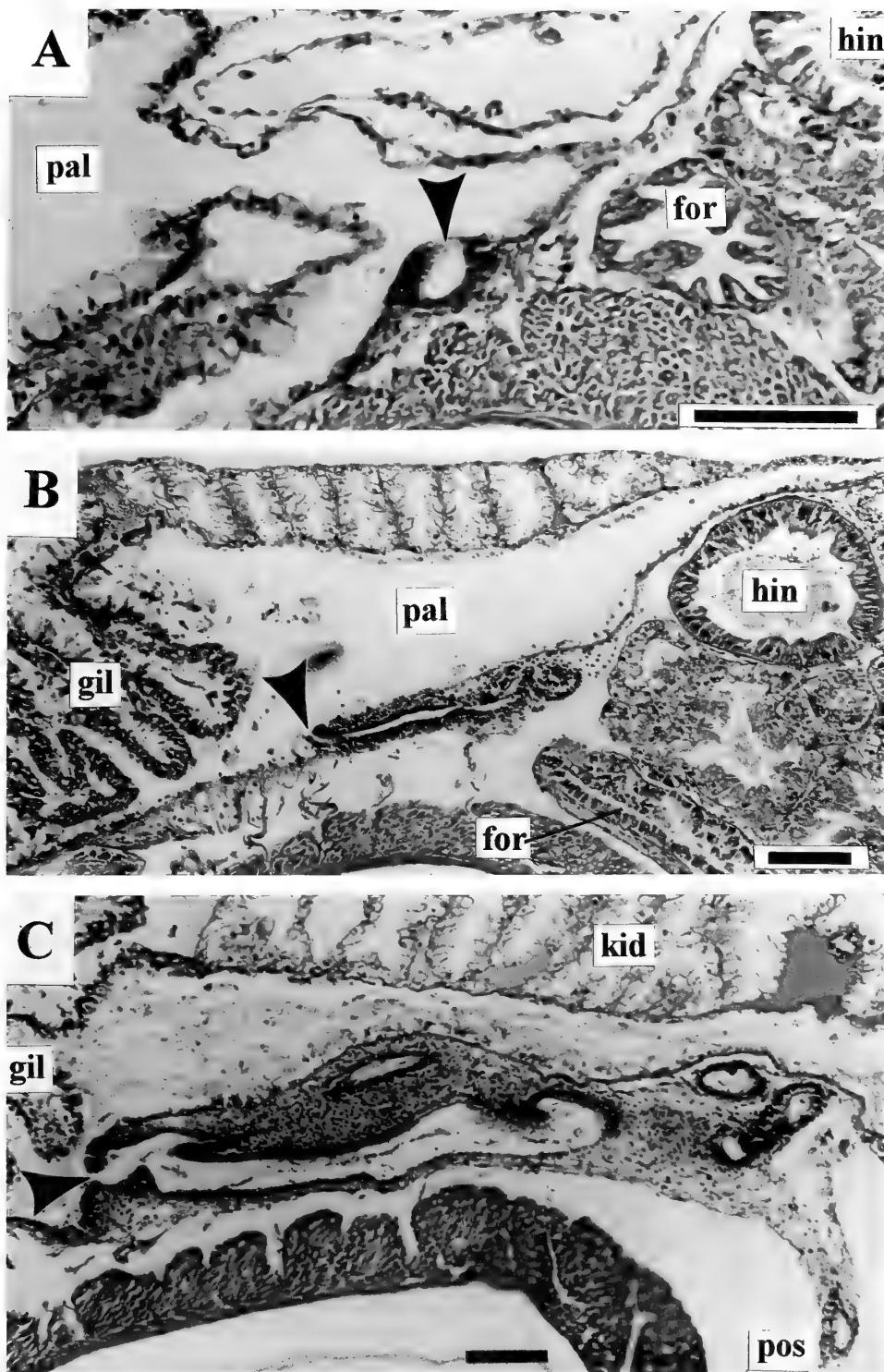


Figure 9. Developing glandular mass in *Bulla striata*, showing location of common genital opening relative to the foregut, hindgut, kidney, and gill. A. 3.4-mm specimen. B. 5.0-mm specimen. C. 7.4-mm specimen. Scale bars = 100 μm . Key: gil = gill; for = foregut; hin = hindgut; pal = pallial cavity; pos = posterior gonoduct; arrow = common genital opening.

Acteocina atrata

The female glandular mass of *Acteocina atrata* is similar to that of *Bulla striata* in several respects; however, the path that the anterior gonoduct takes is quite different. Instead of passing through the mass as in *B. striata*, the gonoduct enters the glandular mass near the common genital opening. All of the glands empty into this same common area.

In this species, the posteriormost portion of the anterior gonoduct immediately following the sphincter has a cuboidal epithelium and is heavily ciliated. It becomes glandular, and forms a loop posterior to the glandular mass, following which there is a second sphincter; this portion is ciliated like the previous one. The epithelium here is cuboidal and is stained light blue. Anteriorly, the gonoduct is nonglandular once again, then enters the base of the sperm-storage pouch following a third sphincter (presumably to prevent the posterior transport of sperm past the pouch). The gonoduct and sperm-storage pouch have thin muscular walls and cuboidal epithelia (Figure 6C). The sperm-storage pouch (Figure 2B [ssp]) is semiserial, in other words, it has separate entrance and exit ducts and is part of the pathway, but is in the form of a diverticulum to one side (cf. two out of three specimens of *Acteocina culcitella* discussed by Gosliner, 1979). Anteriorly, the gonoduct opens broadly into the vestibule.

The vestibule splits posterior to the common genital opening. One portion is the anterior end of the gonoduct, directed ventrally. The other heavily ciliated portion is directed dorsally below the pallial wall, and receives the ducts of the three female glands. The largest and anteriormost is the mucus gland, opening into the vestibule roof. It is histologically similar to the mucus gland in *Bulla striata*, with large cells staining very light blue with hematoxylin (Figure 5D [mug]). The posterior lumen of the gland is U-shaped in cross-section and has short cilia. The albumen and mucus gland walls in this species appear to be about one cell thick, perhaps because of the small adult size.

The membrane gland, smaller and to the left of the mucus gland, has a Y-shaped lumen in cross-section (Figure 5D [mem]). Its epithelial cells are smaller, stain purplish blue, and have short dense cilia. This stains similar to the S-shaped membrane gland in *Bulla striata*, occupies a similar position, and is also relatively small; it is therefore here considered homologous.

The albumen gland lies to the left of the other two glands. It has large epithelial cells with basal nuclei and short cilia, partially stained red with eosin/phloxine (Figure 5D [alb]). As in *Bulla striata*, the posterior part of the albumen gland is located within the "U" of the mucus gland, although their bases are widely separated in this species.

The gametolytic gland of *Acteocina atrata* (Figure 6D [ggl]) is similar to that in *Bulla striata*. Its terminal sac

is adjacent to the pallial wall and pericardium. Its walls are thick, composed of large pink-staining cuboidal cells. In larger specimens, the gland is filled with pink-staining secretions and other purplish-gray material. The gametolytic gland duct is located along the pallial wall adjacent to the gizzard, and enters into the anterior fork of the gonoduct close to the sperm-storage pouch.

Development of the anterior part of the female glandular mass in this species is similar to that in *Bulla striata* in that the glands are present (but undifferentiated) early, and the common genital opening in the smallest specimens is in a different location than at maturity. In the smallest specimen (1.4 mm), the anterior glandular mass is a triangular array of sacs, and the anterior gonoduct passes through the glands rather than being separated from them as in adults. The U-shaped mucus gland is the longest, on the right side of the mass, with the common genital opening lying at its anterior center. A second undifferentiated sac on the left side is probably the incipient albumen gland, and a smaller undifferentiated sac between these two could be the membrane gland. There is no sperm-storage pouch in the smallest specimen. The 1.7-mm specimen has a fully differentiated glandular mass (Figure 8D) with the common genital opening on the right side, and glandular tissue in the anterior gonoduct. The 2.0-mm specimen has a very small amount of sperm in the base of the sperm-storage pouch (Figure 6C [spin]).

Copulatory Organ

The copulatory organ of a cephalaspidean (sometimes called the penis in its entirety, e.g., Gosliner, 1994) opens to the exterior on the right side of the head, in the lateral groove between the cephalic shield and the foot. This leads to an outer duct, here called the penial sheath [after Thompson, 1976; also called penial sac by Lemche (1956), Ghiselin (1966), and Hadfield & Switzer-Dunlap (1984), or male vestibulum by Marcus (1957); Marcus (1957) and Robles (1975) confoundingly labeled the outer wall of the duct-within-a-duct sections the "penial sheath."]. The sheath contains the penial papilla [after Gosliner, 1994; also called glans penis by Lemche (1956) and penis by Thompson (1976) and Mikkelsen (1996)] that sometimes is equipped with hardened spines or ridges [e.g., in *Scaphander* spp. (Marcus, 1974); *Haminoea elegans* (Gray, 1825) (see Marcus, 1958a)]. This in turn leads to a penial extrovert, an ejaculatory duct, and a terminal sac [called spermatic bulb by Hadfield & Switzer-Dunlap (1984) and "root of the penis" by Marcus (1957)]. The gross form, histological structure, and histochemistry of the so-called prostatic gland across Opisthobranchia is especially variable, and has even been implicated in spermatophore formation in Haminoeidae and Runcinidae (Ghiselin, 1966; Hadfield & Switzer-Dunlap, 1984). It is doubtful that all such structures (including

those of caenogastropods) are homologous (Mikkelsen, 1996). Although glandular tissue associated with the copulatory organ might be considered prostatic (e.g., producing sustaining fluid for stored spermatozoa), the terms "prostatic gland" or "prostate" are not used here to avoid the implication of homology with so-labeled organs in other gastropods.

Bulla striata

The adult copulatory organ of *Bulla striata* (Figure 2A [right]) lies relatively loose within the cephalic haemocoel, anchored by a few muscle bundles, and in most specimens coiled dorsally around the buccal mass. Histologically, it is composed of four distinct parts. (1) The penial sheath (Figure 10A) is a longitudinally folded duct leading from the male genital opening. On its wall is a longitudinal gutter delimited by tissue flaps (not seen by Marcus, 1957) and continuous with the external sperm groove running along the animal's right side to the common genital opening. The cross-section of this duct is generally H-shaped through most of its length, and its longitudinal folding renders it expandable to accommodate the evert penis. The walls are muscular, with a partially mucoidal epithelium. (2) At the internal end of the folded duct is the narrowed opening into the next section—a point which has been called the "penial papilla" (Marcus, 1957) (Figure 10B [pep]). This is not a permanent structure, varies in extent, and (as will be described below) does not form the tip of the penis upon eversion. The opening leads to the penial extrovert (so called for reasons that will be obvious below), a wide, longitudinally folded region (Figure 10C) with a non-mucoidal epithelium. Posteriorly, this region is irregularly folded and densely ciliated. The penial extrovert and the penial sheath are embedded within the body wall. The penial extrovert and the following section have a double-walled (duct-within-a-duct) structure; the internal and external walls of the duct are muscular. (3) Also within the double-walled region is the ejaculatory duct, which is a tightly coiled glandular tube (Figure 10D), smaller in diameter than the previous. The epithelium consists of columnar, pale red-staining cells; in the adult stained with PAS, the particles visible in these cells stain magenta. This portion contains stored endosperm in some specimens. (4) Behind the coiled ejaculatory duct, the separated inner and outer walls coalesce, and the copulatory organ ends as a muscular blind sac (Figure 10E), wider in diameter than the double-walled region, and with an epithelium similar to but denser than that of the ejaculatory duct.

The largest adult examined (16.5 mm) is preserved with the penis partially everted to the external opening (Figures 11A, B). From this animal, it is evident that the "penis" is formed of an eversion of the penial extrovert (the second part of the copulatory organ) described

above. In its retracted state, the walls of this portion are folded, and thus are clearly expandable in diameter. The coiled ejaculatory duct in this specimen lies close but not immediately behind the penial tip, and is still somewhat coiled. This duct is narrow in diameter, with non-folded epithelium, and thus appears not expandable. Almost all of the endosperm in this specimen are in the ejaculatory duct rather than in the terminal bulb.

In its early stages (some of the 2.5–5.4 mm specimens), the developing copulatory organ of *Bulla striata* is represented by a long, narrow invagination anterior to the buccal mass (Figure 12A). The wall is thick and densely nucleated overall. The epithelium is cuboidal, unciliated, and also very densely nucleated. The end of the interior lumen is glandular, with pale-red-staining secretory cells. The organ opens anteriorly into a wide chamber, which communicates with the exterior.

In the 5.0-mm specimen, the copulatory organ is slightly longer, although it still does not extend posteriorly to the level of the buccal mass. The double-walled region has differentiated, and the duct ends as a terminal bulb connected to the outer wall (Figure 12B). The epithelia of both interior and exterior ducts are still low, dense, and undifferentiated, except for the end of the terminal bulb. This has a tall, secretory epithelium, with some mucoidal cells and a few dark-red-staining cells interspersed with the paler-red-staining cells present in the smaller individuals.

The 3.3-mm specimen, in spite of its small size, is in a more advanced state of development than those previously discussed. The copulatory organ lies dorsal and to the right of the buccal mass, but is not coiled around it. The penial sheath is only weakly folded. The double-walled region has developed, but the epithelium is undifferentiated, so that the two mature sections of this part (penial extrovert, ejaculatory duct) are not distinguishable. Approximately midway through the inner duct, there is a short section that is U-shaped in cross-section (Figure 12C, arrow). This could correspond to the junction of the penial extrovert and ejaculatory duct of the mature organ. The terminal sac is relatively narrow, about half the width of the double-walled sections (Figure 12D [tes]).

Acteocina atrata

The adult copulatory organ in *Acteocina atrata* (Figure 2B [right]) opens to the exterior on the right side of the head, and coils around the buccal mass as in *Bulla striata*. It is relatively simple in gross morphology, but is extremely long, coiling extensively within the anterior body cavity. External and dorsal to the male genital opening, there is a small smooth purple-staining area along the body wall that is consistently present but of unknown nature (mucoidal? cuticular?) and function. Histologically, the copulatory organ has three distinct portions. (1) The outermost penial sheath is similar to that in *Bulla*

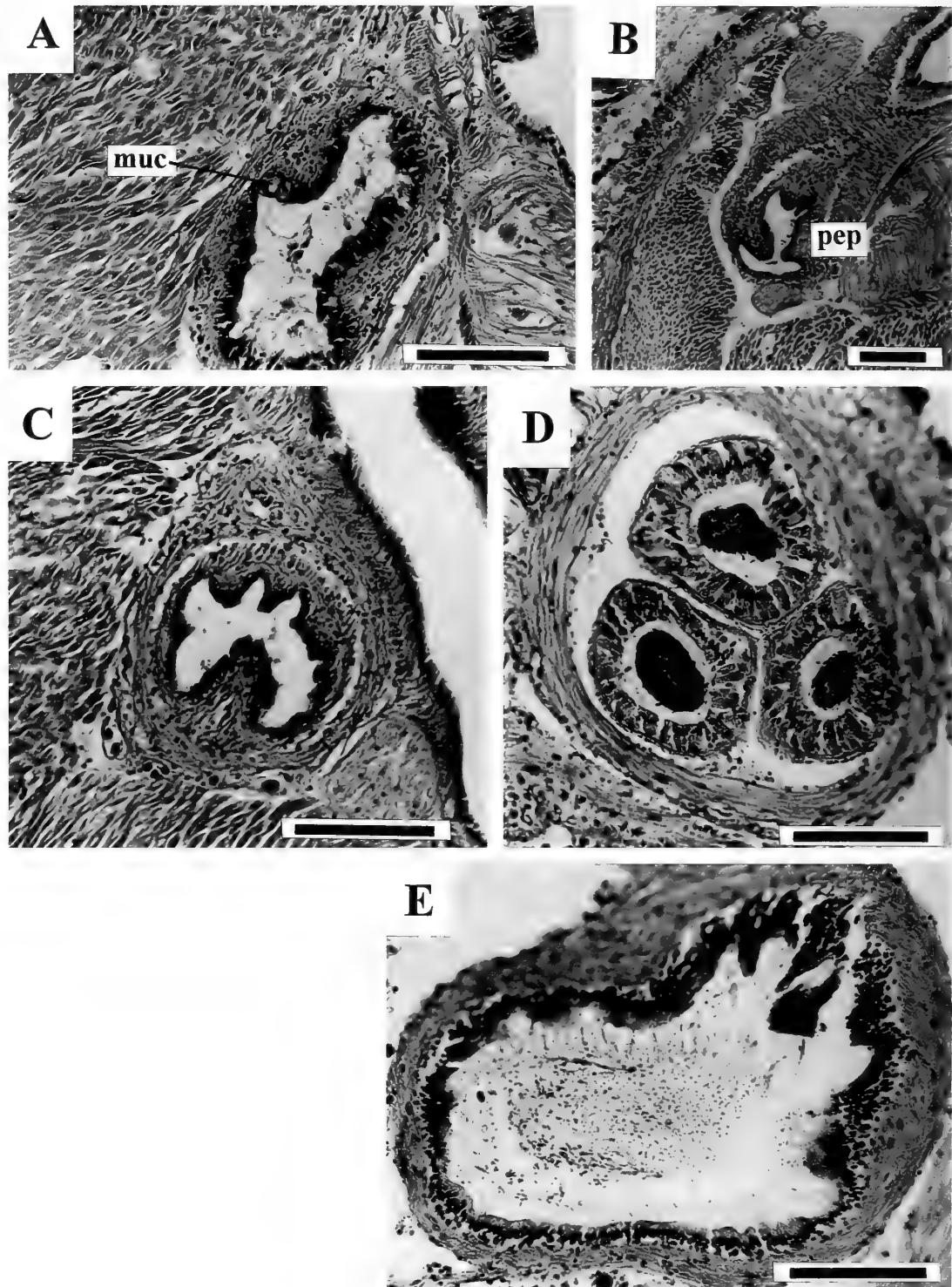


Figure 10. Copulatory organ of *Bulla striata*. A. Cross-section of penial sheath (FK-163; 11.2-mm specimen). B. Tangential section of retracted copulatory organ, showing "penial papilla" (FK-163; 7.4-mm specimen). C. Cross-section of penial extrovert (FK-163; 11.2-mm specimen). D. Cross-section through coiled (prostatic) ejaculatory duct (PSM-767; 16.5-mm specimen). E. Tangential section of terminal sac (PSM-767; 16.5-mm specimen). Scale bars = 100 μm . Key: muc = mucus cells; pep = "penial papilla."

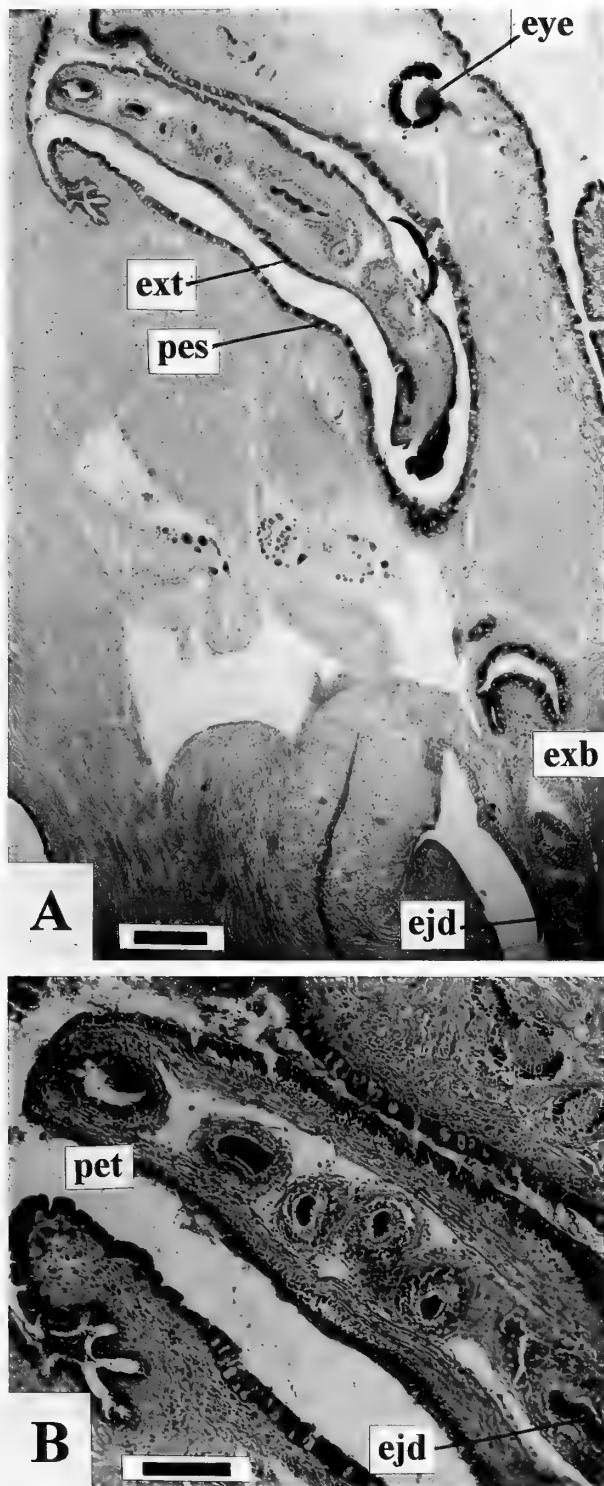


Figure 11. A. Partially everted penis in *Bulla striata* (PSM-767; 16.5-mm specimen). B. Same, penial tip (enlarged). Scale bars = 100 μm (B); 200 μm (A). Key: ejd = ejaculatory duct; ext = extrovert (wall); exb = base of extrovert; eye = right eye; pes = penial sheath (wall); pet = penial tip.

striata, in being H-shaped in cross-section and somewhat muscular, but it is not mucoidal (Figure 13A). The walls become irregularly folded as one proceeds interiorly, and grade without sharp demarcation into the (2) wider medial section. No definitive penial papilla is present at this junction in all seven specimens sectioned for this study. The epithelium of the medial section is unusual; the wall itself is thin and flat, but has large papillae composed of distinct clumps of tall cells with central nuclei (Figures 13B [pap], C [med]). These become still larger internally, where small amounts of stored endosperm are present in some specimens. The terminus of the copulatory organ is (3) an elongated sac, delimited from the medial section by a slight constriction, and with thick, secretory, non-folded walls (Figure 13C [tes]). The epithelial cells are ciliated and stained red, with large basal nuclei; near the blind end, the sac narrows slightly, and there are no cilia.

The copulatory organs of juvenile *Acteocina atrata* are very similar to those of juvenile *Bulla*, at a stage before the double-walled region develops. The smallest animal (1.4 mm) has an elongated invagination that ends just anterior to the buccal mass (Figure 13D). The epithelium is cuboidal and unciliated, with large, dark nuclei. There are no glandular epithelia evident in the copulatory organ of this juvenile. The other 1.4-mm juvenile is in a more advanced stage of copulatory organ development, with some glandular tissue present.

DISCUSSION

Ontogeny of the Cephalaspidean Gonoduct

The heterobranch gonoduct, like that of caenogastropods, develops from several ontogenetic components, including both ectodermal and mesodermal tissues. In opisthobranchs, there are generally three components, including the male copulatory organ, the female glandular mass, and the posterior gonoduct (Moor, 1983). The copulatory organ and glandular mass develop as ectodermal invaginations, and the gonad develops from mesodermal tissues.

Bulla striata and *Acteocina atrata* are consistent with this general pattern. The copulatory organ develops as an invagination of the ectodermal body wall. The ectodermal glandular mass and mesodermal posterior gonoduct are already formed and continuous in the smallest specimens examined in this study, so the point of fusion between these components could not be definitively demonstrated. However, the smallest specimens of *B. striata* showed a distinct change in the structure of the gonoductal epithelium, which is otherwise undifferentiated, just behind the glandular mass in the region where the sphincter develops. This supports the hypothesis that the adult sphincter represents the point of fusion between the different parts of the duct.

Other heterobranchs display similar developmental patterns. In *Tritonia hombergi* Cuvier, 1803 [Sacoglossa:

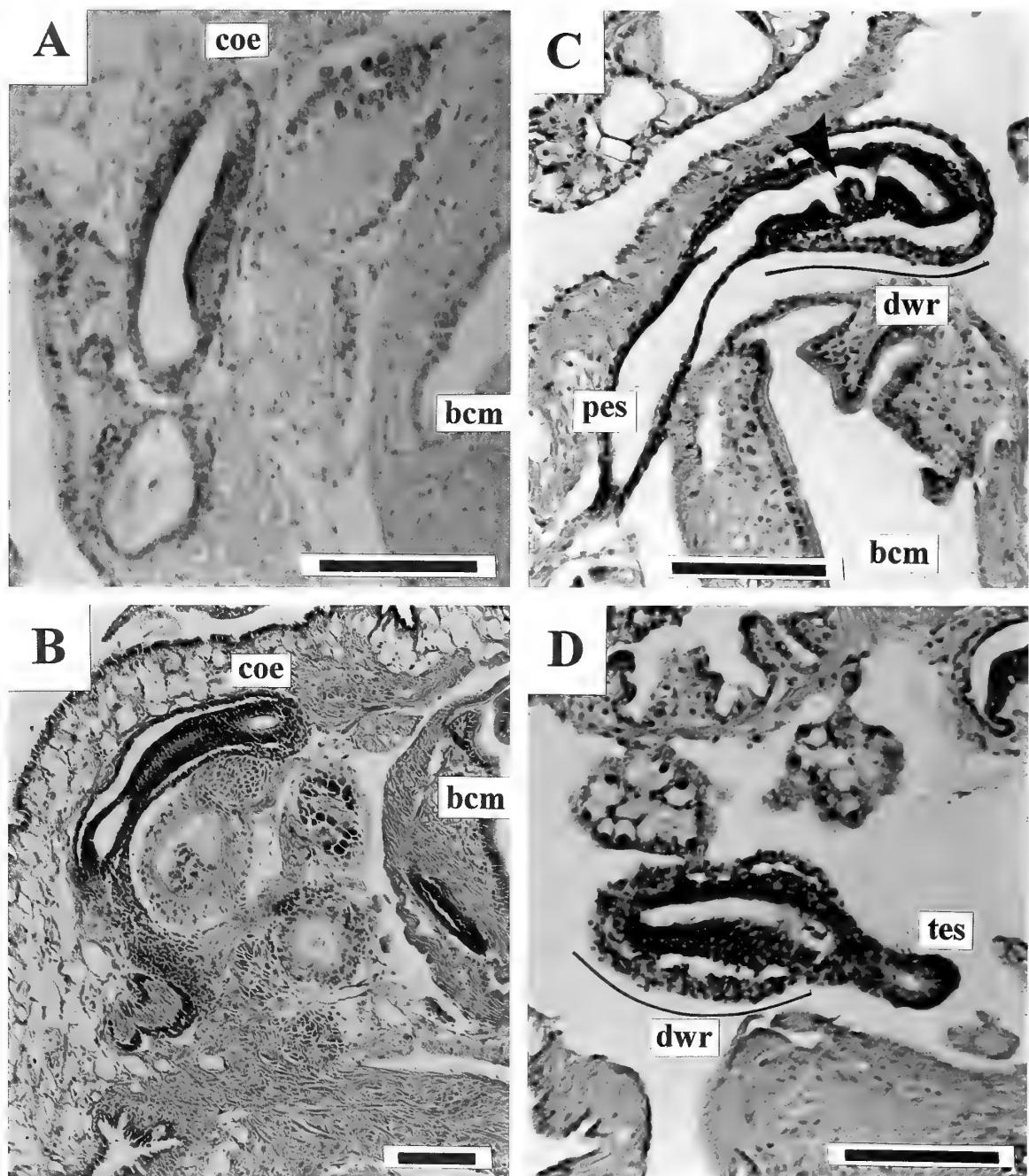


Figure 12. Development of copulatory organ of *Bulla striata*. A. Tangential section, invagination stage (FK-163; 3.4-mm specimen). B. Tangential section, double-walled duct stage (FK-163; 5.0-mm specimen). C. Tangential section, advanced double-walled duct stage, showing partial differentiation of inner duct (FK-211; 3.3-mm specimen). D. Tangential section, advanced double-walled duct stage, showing small terminal sac (FK-211; 3.3-mm specimen). Scale bars = 100 μm . Key: bcm = buccal mass; coe = end of copulatory organ; dwr = double-walled region; pes = penial sheath; tes = terminal sac; arrow = possible junction of extrovert and ejaculatory duct.

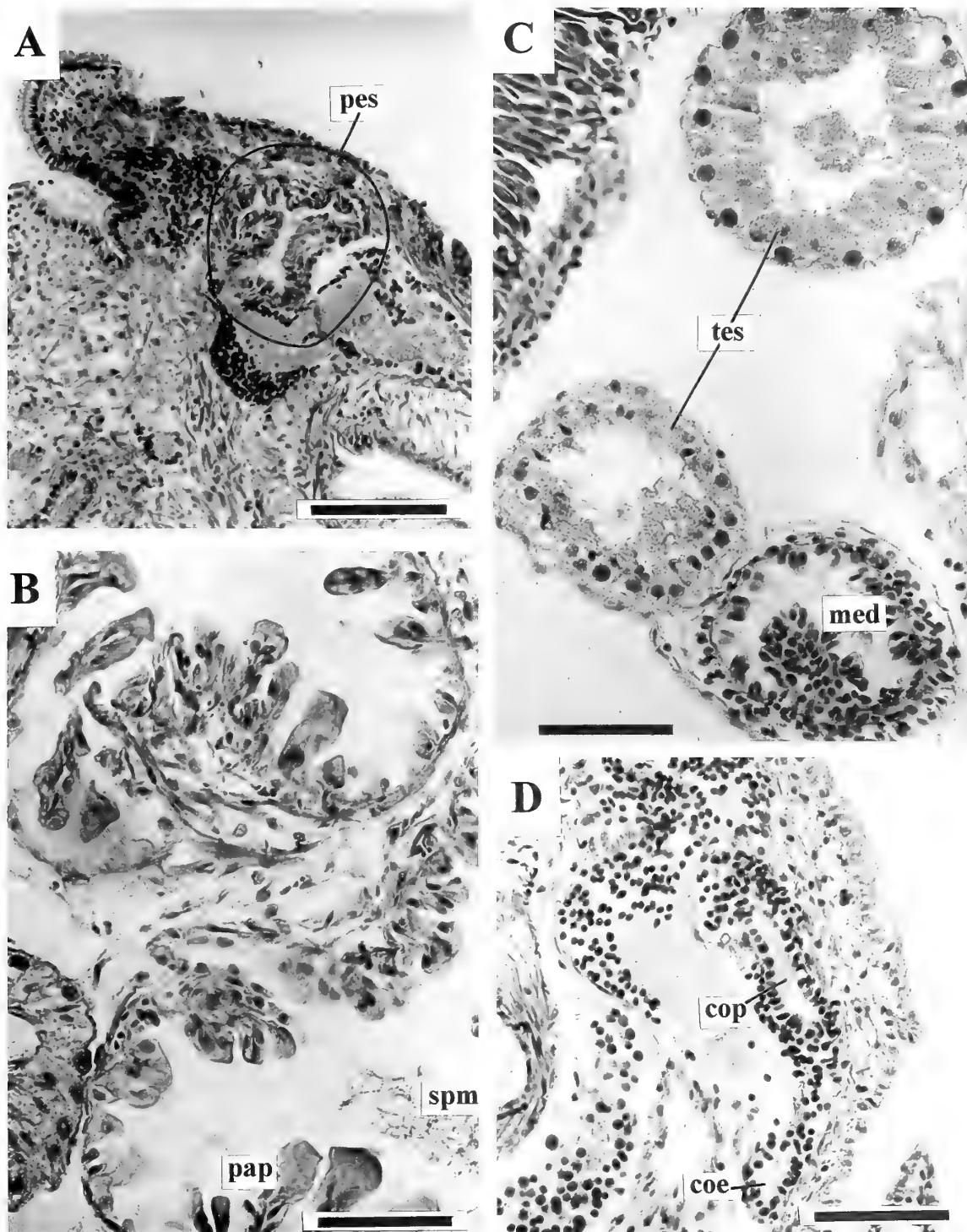


Figure 13. Copulatory organ of *Acteocina atrata*. A. Cross-section of the penial sheath (3.2-mm specimen). B. Tangential section of medial region, containing sperm (3.1-mm specimen). C. Cross-section of medial region and terminal sac (2.0-mm specimen). D. Tangential section of developing copulatory organ, invagination stage (1.4-mm specimen). Scale bars = 50 µm (B–D); 100 µm (A). Key: coe = end of copulatory organ; cop = copulatory organ; med = medial region; pap = papillae; pes = penial sheath; spm = sperm; tes = terminal sac.

Tritoniidae], the anterior parts of the gonoduct appear as a single invagination of the body wall, and fuse with the rudiment of the posterior gonoduct directly posterior (Thompson, 1962); a sphincter or valve is present in this location in adults (Thompson, 1961). Pulmonates (and many opisthobranchs) are more complex as adults because of the independent development of male and female parts of the gonoduct, but appear to display similar development. Fraser (1946) found three ontogenetic components in the reproductive system of *Lymnaea stagnalis appressa* Say, 1821 [Pulmonata: Lymnaeidae], including two ectodermal components forming the male and female ducts, respectively.

Lemche (1956) included some discussion of gonoduct development in *Cylichna cylindracea* (Pennant, 1777) in the form of a description of the gonoduct in a single subadult specimen of unknown size. The reproductive anatomy of this specimen differs little from that of the adults examined. Glandular tissues are starting to differentiate, particularly in the posterior loop of the anterior gonoduct, the gametolytic gland (= spermatocyst of Lemche) and in the albumen gland. The mucus gland (= nidamental gland of Lemche) has not started to develop secretory tissues. *C. cylindracea* shows similar developmental characteristics to subadults of the two species studied here, but more data will be needed to compare other stages.

Caenogastropods, the sister group to heterobranchs (Ponder & Lindberg, 1997), also have two or more reproductive system components, but these differ from those of heterobranchs. The posterior gonoduct is very similar in the two groups. The heterobranch ampulla is functionally and histologically similar to the seminal vesicle in male caenogastropods, and could be homologous. Ponder & Lindberg (1997) reached a similar conclusion, however noted that the seminal vesicle is modified or lacking in many basal heterobranchs. The development of the copulatory organ from a separate *anlage* occurs in some heterobranchs, including the species examined here, similar to the independent initiation of development of the penis and its duct seen in some caenogastropods, e.g., *Littorina saxatilis* (Olivi, 1792) [Littorinidae], discussed by Guyomarc'h-Cousin (1976), and *Crepidula adunca* Sowerby, 1825 [Calyptaeidae], described by Moritz (1939). The differentiation of the anterior gonoduct differs most strongly between heterobranchs and caenogastropods. In heterobranchs, it develops from a single ectodermal *anlage*, unless it is connected to the copulatory organ, in which case the two portions develop separately and fuse (e.g., *Lymnaea*; Fraser, 1946). In caenogastropods, the same region can develop from two or more *anlagen*, especially if both ectodermal and mesodermal components are included, such as is the case in *Viviparus viviparus* Linnaeus, 1758 [Viviparidae] (see Drummond, 1902).

The location of the common genital opening in both species examined in this study shifts markedly during on-

togeny, from an original medial position near the foregut and pericardium to a more lateral position on the right side of the gizzard. The change in location is related to the development of the vestibule, and could (like "detorsion" in these animals) be related to differential growth and lateral migration of the pallial cavity (Brace, 1977; Mikkelsen, 1996). It is tempting to suggest that the original position of the opening is primitive because it is similar to the location of the pallial gonoduct opening in caenogastropods. Insufficient data are available to address this issue, but if this is not related to an evolutionary change in position, then some other reason will be necessary to explain the shift.

Comparison of *Bulla striata* and *Acteocina atrata*

The adult reproductive anatomy of *Bulla striata* and *Acteocina atrata* differs most strikingly in the morphology and development of the copulatory organ. *B. striata* has a very complex copulatory organ, and its function, in light of the partially everted specimen discussed herein, is relatively clear. The copulatory organ of *A. atrata* appears relatively simple (although the epithelium of the medial section is unique), and the mechanism of its function is not obvious. Developmentally, the copulatory organs of the two species are similar only during the earliest stage, when they consist of undifferentiated invaginations. Otherwise, the only histological similarity between them is the eosinophilic glandular tissues in the ducts and terminal sac, and in the general morphology of the penile sheath. Ghiselin (1966) stated that opisthobranch prostatic glands can be recognized in part by their eosinophilic secretions (probably consisting mostly of protein), which is consistent with the tissues observed in these two species. It is reasonably assured that in *B. striata* and *A. atrata* these tissues are prostatic (without calling them prostatic glands) and are homologous, in spite of their gross morphological differences.

Another major difference between *Bulla striata* and *Acteocina atrata* is the relative involvement of the gonoduct in the mature glandular mass. In *B. striata*, the anterior gonoduct travels through the glandular mass and intercepts each gland separately at its base. In *A. atrata*, the gonoduct is entirely free of the three large glands on a single diverticulum [also noted in this genus (as *Cyllichnella*) by Gosliner, 1979]. In the smallest specimen of *A. atrata* examined, however, the gonoduct does pass through the glandular mass.

The two species display different organogenetic timing (Table 1). In *Acteocina atrata*, different parts of the reproductive system develop more or less contemporaneously. This species appears to be protandric in the sense that it is anatomically able to function as a male before it can function as a hermaphrodite. This is in agreement with Gosliner (1994) who considered protandry the typical condition in opisthobranchs. Sperm production and

maturity of the copulatory organ begins before egg production and maturation of the glandular mass, perhaps because of the investment required by the egg's large size and nutrient load. Immature animals (i.e., the 2.0-mm specimen) also had small amounts of sperm in the anterior sperm-storage pouch. In *Bulla striata*, the copulatory organ matures much earlier than the glandular mass, but sperm production in the gonad does not appear to do so.

Within the series of sectioned *Bulla striata*, individuals from different populations appeared to develop at different rates. The two smallest specimens, from station FK-211, were at the same stage of organogenesis as individuals nearly twice as large from FK-163. This difference could be seasonal; FK-211 was made in April at the transition between cool spring and hot summer, while FK-163 was made in September in the hottest part of the summer.

The overall structure of the female glandular mass is similar in the two species, although not identical. The similar histology and early development of the albumen and mucus glands are striking, particularly in the nesting of the albumen gland within the 'U' of the mucus gland. This is also apparent in members of *Cyllichna* (see Lemche, 1956). The membrane glands in *Bulla striata* and in *Acteocina atrata*, although differently shaped, appear homologous due to similar locations, structures, and staining properties. Ghiselin (1966) reported that nudibranch egg membranes stain less strongly with hematoxylin than do their mucus layers. Thus the mucus glands in sections might be expected to stain darker than membrane glands. They did not in this study, leaving some doubt in the application of the labels and function of these glands.

Of the two sperm sacs associated with the female glandular mass, the gametolytic gland is almost certainly homologous in the two species; however, it is interesting to note that the point of entry into their respective gonoducts is different. In juvenile *Bulla striata* and in *Acteocina atrata* of all sizes, the gametolytic gland duct enters the gonoduct anteriorly. During development in *B. striata*, however, the entrance of the duct is moved to the posterior vestibular wall.

Homology of the Cephalaspidean Gonoduct

Homology of the various components of the cephalaspidean reproductive tract relative to those of other gastropods is a clear priority in heterobranch phylogenetics, but is still elusive. Ghiselin (1966:fig. 1C) diagrammed the reproductive system of a hypothetical ancestral opisthobranch for comparison with idealized gonochoric prosobranchs as presented by Fretter & Graham (1994).

Ghiselin's (1966) hypothetical organization claimed the presence of a pallial prostate in the ancestral opisthobranch (undoubtedly in reference to the once-cephalaspidean *Acteon*, now considered a lower heterobranch; Mikkelsen, 1996). The so-called prostatic glands of the

male portion of the reproductive tract are especially problematic for homologous considerations. Prostatic glands of caenogastropods (also of the former cephalaspideans *Acteon* and *Hydatina*; Mikkelsen, 1996) are pallial, along an internal spermiduct leading to the base of the penis, and there is often additional secretory epithelium in the penile duct. Penial and pallial prostates develop very differently, although both are ultimately derived from ectodermal tissues. Although the penial prostatic glands of *Bulla striata* and *Acteocina atrata* are probably homologous, their relationship to similarly labeled structures in other gastropods will require detailed study.

Hadfield & Switzer-Dunlap (1984:234) commented that the gonoduct of bulloideans is more similar to that of anaspideans than to that of philinoideans. This statement would be phylogenetically interesting to corroborate, in view of the close relationship of the cephalaspidean Bulloidea to the Anaspidea (Mikkelsen, 1996). However, comparison of the reproductive system of *Aplysia* (see Thompson & Bebbington, 1969) does not offer strong encouragement. Like most cephalaspideans, *Aplysia* has a proximal seminal receptacle, absent in both of the species examined herein. The distal sperm-storage pouch (near the common genital opening) in these two species is similar to a distal "seminal receptacle" in *Umbraculum* [Notaspidea] (Schmekel, 1985:fig. 7), and a distal "exogenous sperm sac" in some members of Aglajidae [Cephalaspidea: Philinoidea] (Rudman, 1974). In these last two examples, all of the components of the female glandular mass join the gonoduct near the vestibule, as is true in *Acteocina atrata* studied here. This area can justifiably be called the "fertilization chamber" in such species.

As in *Acteocina*, *Bulla striata* examined here has a sperm-storage pouch near the common genital opening. The pouch in the largest specimen (16.5 mm) contained a small amount of embedded oriented sperm, but we have avoided the label "seminal receptacle" for reasons explained earlier. Whether these pouches are homologous with each other, with the similarly located seminal receptacles of *Umbraculum* or Aglajidae, or with the proximal receptacles of any of the caenogastropods, is unknown. Histological characterization of the tissue walls in the two species examined here (relative to the cellular definitions by Schmekel, 1971) was inconclusive. The pouch of *Acteocina atrata* is semiserial with the anterior gonoduct, differs histologically, and did not contain oriented sperm in any of the sectioned specimens. Gosliner (1979) found "semiserial or serial" to vary in several species of *Acteocina*, so this difference does not seem informative.

Gosliner (1994:320) claimed that a seminal receptacle was "clearly absent" in a number of opisthobranch taxa, including *Bulla*. This statement might be more reflective of position than of histological structure—*Bulla striata* has no pouch on the pallial gonoduct where the receptacle "should be" (i.e., between the ampulla and the female

glandular mass; Ghiselin, 1966; Gosliner, 1994). The presence of a seminal receptacle within the tissues of the female glandular mass was reported by Robles (1975) and Mikkelsen (1996); no such structures were observed in this study. So-called seminal receptacles, defined either by location or by the presence of oriented sperm, also bear homology questions in caenogastropods and neritopines (Ponder & Lindberg, 1997).

Potential homology between the heterobranch gametolytic gland and the caenogastropod bursa copulatrix has been mentioned by several authors (e.g., Ghiselin, 1966; Hadfield & Switzer-Dunlap, 1984; Gosliner, 1994; Mikkelsen, 1996). Such a relationship is supported by this study by the initial location of the gametolytic gland duct at the common genital opening in *Bulla striata*, similar to the location of the bursa in caenogastropods.

Cephalaspideans are well known for depositing fertilized eggs in the laboratory, long after a mating event could have occurred, suggesting that they are well equipped for sperm storage. One specimen of *Bulla striata* examined here suggests a possible scenario. This adult (11.4 mm) contained sperm in the anterior gonoduct but none in the sperm-storage pouch. It is thus likely that the small sperm-storage pouch near the opening is not a bursa copulatrix, and that the anterior gonoduct itself is used for short-term storage of exosperm after mating. The sperm-storage pouch, by evidence of the oriented sperm in one large specimen, seems to be for long-term storage. But whether these are exosperm or endosperm is unknown.

The homologies of the female reproductive glands in heterobranchs and caenogastropods are unclear. Heterobranchs are thought to have three female glands, putatively responsible for producing the three layers of the egg coatings: albumen, membrane, and mucus, from egg to exterior (Ghiselin, 1966). Caenogastropods have two female glands, the albumen and capsule glands. [It must be stressed that although "egg capsules" and even "capsule glands" are occasionally described in opisthobranchs (e.g., Rudman, 1971; Robles, 1975; Mikkelsen & Mikkelsen, 1984), opisthobranch egg capsules are without doubt not chemically identical or homologous to the hardened external egg capsules common in caenogastropods.] The staining reactions of these can differ considerably from one investigation to another, in large part because researchers rarely use the same histological methods. Additionally, neogastropod reproductive glands often have many differently staining regions within the same mass of glandular tissue (Fretter, 1941; Houston, 1976). Albumen glands are present in both caenogastropods and heterobranchs, but whereas heterobranch albumen glands produce mostly neutral carbohydrates (Ghiselin, 1966), albumen of caenogastropods consists of proteins and mucopolysaccharides (Fretter & Graham, 1994). Thus analogous glands have different products and staining prop-

erties in addition to different morphologies, and their homologies across higher gastropod taxa are doubtful.

Functional Morphology

It is a well established fact that the male copulatory organ of cephalaspids (and most other opisthobranchs) is retractile (also called protrusible; Hadfield & Switzer-Dunlap, 1984; Gosliner, 1994; and others). However, we have little real evidence on how this organ everts to transfer sperm to the mating partner. Some data are available from Marcus (1974:figs. 63, 64), who figured the retracted and everted copulatory organ of *Scaphander darius* Marcus & Marcus, 1967. The fortuitous sectioning during this study of an adult *Bulla striata* with a partially everted copulatory organ, coupled with sections of the organ in full retraction, here provides some of the best functional data for cephalaspids.

The adult copulatory organ in *Bulla striata* was described briefly and figured by Marcus (1957:395, fig. 6). Those of *B. solida* Gmelin, 1791 (Marcus, 1976:fig. 10) and *B. gouldiana* (Marcus, 1961:fig. 4) are comparable. The specimens examined here agree reasonably well with previous interpretations, although some of the terminology (most of which implies function) is misleading. The longitudinally folded outermost duct, here called the penial sheath, is appropriately labeled once the penis has fully everted, although (contrary to Marcus, 1957) there is no permanent penial papilla in *B. striata*. Marcus (1957) also labeled the coiled ducts in *B. striata* the prostatic gland, and it is true that this portion has secretory epithelium and stores sperm. However, it has no subepithelial glandular tissue, and it could be argued that it is not a "gland" per se. The terminal bulb is similarly secretory and also appears capable of storing sperm. It could by this evidence be considered an expanded extension of the prostatic gland. To be conservative, however, we continue to label it separately here. It is consistently as wide as the double-walled region in adult *B. striata*, but is only a tiny terminal caecum in immature specimens. Tiny end bulbs were also described on the copulatory organs of *B. gouldiana* [see Bergh, 1901 (as *B. ampulla* var. *nebulosa* Gould in A. Adams, 1850); Marcus, 1961; Robles, 1975] and *B. solida* (see Marcus, 1976)]. Marcus (1961) claimed the end bulb was sometimes absent in *B. gouldiana*, which led Ghiselin (1966) to surmise that its full expression might only occur during breeding condition. It is equally possible that the diminutive bulbs described by earlier authors were all based on immature animals.

Penial eversion in *Bulla striata* is probably accomplished by a combination of muscular action and hydrostatic pressure—the longitudinal/circular muscles of the walls of the copulatory organ contract to force fluid (contained between the inner and outer ducts of the double-walled sections) outward. The laterally attached penial

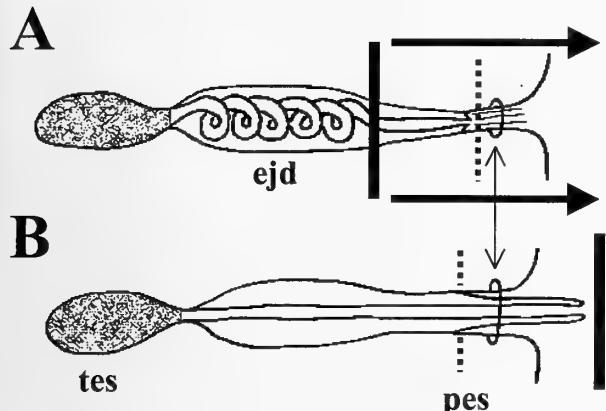


Figure 14. Diagrammatic copulatory organ of *Bulla striata*, showing retraction (A) and eversion (B). Key: ejd = ejaculatory duct; pes = penial sheath; tes = terminal sac; dashed line = base of everted penis; ring = diameter of penial sheath, showing expansion during penile eversion; solid line = penial tip.

retractor muscle(s) could also play a role. It is the longitudinally folded non-mucoidal penial extrovert that “turns inside out” to become the functional penis. This is similar to eversion in *Scaphander darius*, although the “turning” is one-sided, as evidenced from the figures of Marcus (1974:figs. 63, 64), resulting in a lateral open groove. In *Bulla*, the penial sheath expands to accommodate the evertting structure (and might itself also evert), but it does not alone “serve as a penis” as explained by Hadfield & Switzer-Dunlap (1984:234). The “penis” of *B. striata* when fully everted has an outer wall composed of the “inside out” penial extrovert, and an inner duct of the uncoiled (prostatic) ejaculatory duct (Figure 14). The ultimate penial tip is the junction between these two sections.

The copulatory organ of *Acteocina atrata* differs markedly from that of *Bulla striata*, and cannot function in the same way. It does not have the double-walled, duct-within-a-duct construction, which would allow hydrostatic pressure to operate, nor does it have a coiled duct capable of extending. The structure as a whole is not as muscular as that of *B. striata*, but there are some longitudinal and circular muscles associated with the penial sheath and medial sections. It does have a longitudinally folded penial sheath, which appears capable of expanding when some part of the structure is everted. A similar configuration was figured by Marcus (1958a:fig. 32, as *Tornatina*) for *A. canlei* (d’Orbigny, 1941) and by Marcus (1977:fig. 53) for *A. inculta* (Gould, 1855), albeit with slightly more definitive penial papillae. No penial papilla was confirmed in *A. atrata*, although its presence has been previously noted in this and other philinoideans (e.g., Marcus, 1958b, 1974, 1977; Mikkelsen, 1996). From our data and Marcus’ (1958a; 1977) figures, it seems possible that the penial sheath “turns inside out”

to allow the medial section to push outward through its lumen. This is the mechanism supposed by Marcus (1958a). The medial section would thus be called the ejaculatory duct, although its unusual epithelium precludes homology with the ejaculatory duct of *Bulla*. It is also unknown whether or not the medial section also “turns inside out.” A terminal sac is certainly present [contrary to Hadfield & Switzer-Dunlap (1984) who claimed that members of Philinoidea (including *Acteocina*) lack a spermatic bulb], although its function is uncertain. It is similarly extremely long in *A. eximia* (Baird, 1863) (Marcus, 1977:fig. 58). Further study of reproductive structure and function in Acteocinidae is warranted.

The routes of sperm and ova travelling through the mature gonoduct of the two species studied here are not completely clear; however, the morphological differences between the two species imply different pathways. Ghiselin (1966) noted that the products of the three female glands must be applied to exiting eggs in the order that they are found in the egg mass, i.e., albumen, membrane, mucus. This order was confirmed by the sequential intersections of the three glands with the pallial gonoduct in *Bulla striata*. The glands of *Acteocina atrata* have a common duct, so it is more difficult to interpret in this case. In *B. striata*, it appears likely that the albumen gland functions as a diverticulum because its lumen is quite small and is probably not capable of accommodating inward and outward tracts of ova. Robles (1975) found this to be the case in *B. gouldiana*, in which eggs passed through the membrane and mucus glands (but not through the albumen gland). Ghiselin (1966) noted that this had been also demonstrated in Anaspidea and Sacoglossa, the two closest sister groups of Cephalaspidea (Mikkelsen, 1996). The mucus gland of *B. striata*, on the other hand, has an extremely wide opening. The lumens of all three glands (albumen, mucus, membrane) are ciliated in both species. Schmekel (1985) noted that eggs pass through the membrane and mucus glands of all opisthobranch taxa thus far studied. Living animal studies, or techniques for preserving specimens in the act of mating and/or egg deposition (e.g., Robles, 1975) will be necessary to confirm the exact pathways.

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A New Species of the Aporrhaid Gastropod Genus *Goniocheila* Gabb, 1868, from the Late Oligocene of North Carolina

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Abstract. Description of the new species *Goniocheila wilsoni* increases to three the number of species of this aporrhaid genus present in the Gulf Coast and southern Atlantic Coast Oligocene faunas of North America. *Goniocheila wilsoni* clearly exhibits characteristics of *Goniocheila* Gabb, a genus that has from its inception been considered close to *Aporrhais*, *Arrhoges*, and widely recognized European Paleogene aporrhais close to or referred to “*Aporrhais*” *sowerbii* and “*Aporrhais*” *speciosa*. These species have been referred to *Aporrhais*, *Drepanocheilus*, and *Goniocheila*; and “*A.*” *speciosa* s.l. has been considered to include forms having a multidigitate wing as in *Aporrhais*, as well as an unidigitate wing as in *Drepanocheilus*. *Goniocheila* shares more characteristics with *Drepanocheilus*, especially early Tertiary *Drepanocheilus*, than with *Aporrhais* and *Arrhoges*.

INTRODUCTION

An undescribed species of *Goniocheila* Gabb, 1868, from the “Silverdale beds” was mentioned by MacNeil (in MacNeil & Dockery, 1984), but the specimens available to him were inadequate to serve as the basis of a species. Richard and Liz Petit recovered excellent specimens of this species, herein described as *Goniocheila wilsoni*, from the “Silverdale beds” on Webb Creek, Silverdale, Onslow County, North Carolina.

The “Silverdale beds” were included in the Belgrave Formation by Ward et al. (1978), and the Belgrave Formation was considered to be of earliest Miocene age. However, the Haywood Landing Member (= the “Silverdale beds”) of the Belgrave Formation is now dated as latest Oligocene, late Chattian stage (Rossbach & Carter, 1991, planktic foraminifera zone N 3; Ward, 1992, Depositional Event 1).

In North America only two other species of *Goniocheila* have been recognized: *Goniocheila lirata* (Conrad, 1848) the type species, and *G. menthafontis* (MacNeil, in MacNeil & Dockery, 1984) are both from the Vicksburg Group in Mississippi and of earlier Oligocene age, *G. lirata* being from the Byram Formation and *G. menthafontis* from the Mint Spring Formation. The new species is readily recognized as congeneric with *G. lirata* and *G. menthafontis*, and *G. wilsoni* is especially similar to *G. menthafontis*.

Position of *Goniocheila* relative to other aporrhais is less clear. MacNeil (in MacNeil & Dockery, 1984) con-

sidered *Goniocheila* to be a subgenus of *Aporrhais* da Costa, 1778, as had Gabb (1868) when erecting the taxon. MacNeil also placed in *Goniocheila* all 10 of the Paleogene species referred to *Aporrhais* by Wrigley (1938)—including English Paleogene specimens identified as *Aporrhais speciosa* (Schlotheim, 1820), thus suggesting the inclusion of many European forms ranging in age from late Paleocene to late Oligocene in *Goniocheila*. Wenz (1940) placed *Goniocheila* as a subgenus of *Drepanocheilus* Meek, 1864, and Báldi (1973) placed “*A.*” *speciosa* in *Drepanocheilus* rather than in *Aporrhais*. MacNeil characterized *Aporrhais* (*Aporrhais*) as an aberrant group with fewer species and shorter geologic range than *Goniocheila*, but he did not define the geologic range of *Aporrhais* or *Goniocheila*. Several revisions of Tertiary chronologies cause Wrigley’s “Eocene and Oligocene” species to be late Paleocene to late Eocene in age (e.g., Davies, 1975; Berggren, 1972; Berggren et al., 1985; Curry, 1992).

Roy (1994) indicated that *Aporrhais*, was present in the Cenomanian, thus giving it greater geologic range than *Goniocheila*. Furthermore, he divided aporrhais into two groups: “M1” characterized by multidigitate wings, and including *Aporrhais*, and “M2” characterized by those with simple wings, and including *Arrhoges*, *Goniocheila*, and *Drepanocheilus*. Several European workers (e.g., Glibert, 1957; Báldi, 1973; Lozouet, 1986; Gitton, et al., 1986) have included within “*Aporrhais*” *speciosa* s.l. forms with both types of wing margins.

Characteristics of the European Paleogene species distributed among *Aporrhais*, *Arrhoges*, and *Drepanocheilus* by various workers are difficult to evaluate because many older descriptions are incomplete, and some figures do not clearly show the morphologic features. European workers studying this group of aporrhaid have not commented on a resemblance to *Goniocheila*, although Lozouet (1986) notes the Oligocene presence of *Goniocheila* (as a subgenus of *Aporrhais*) in Mississippi. Nor have European workers commonly recognized a generic distinction (or even a specific distinction) among forms having a multidigitate rather than a simple outer lip. Conversely, the multidigitate wing is viewed as being derived from the simple outer lip (Lozouet, 1986). *Goniocheila* is most similar to *Drepanocheilus* using the characteristics of Table 1, but with its outer lip features ignored is most similar to *Aporrhais* (Table 2).

The fauna of the Haywood Landing Member of the Belgrade Formation in North Carolina has a tropical aspect, having provided a large number of unusual genera and species of muricids (Vermeij & Vokes, 1997). Rossbach & Carter (1991) suggested a climate for North Carolina Oligocene faunas similar to that of today with warm temperate mollusks inshore and more tropical forms at depths exceeding 25 m. They recognized a reduction in tropical genera between the faunas of the Lower River Bend Formation of early Oligocene age and the Upper River Bend Formation of late Oligocene age, and a further reduction in the fauna of the Belgrade Formation which shows an even stronger Western Atlantic influence. The rarity of *Drepanocheilus*, *Aporrhais*, and *Goniocheila* in late early and middle Eocene faunas (MacNeil in MacNeil & Dockery, 1984) is perhaps related to a warming climate in the early Eocene, and the return of these aporrhaines, to a cooling climate in the Oligocene. Lozouet (1986) commented on the loss of aporrhaid in the Eocene and their abundance in the European Oligocene. Sohl (1967) noted that although *Drepanocheilus* is widely distributed, it is much more abundant from cooler water faunas than from subtropical and tropical faunas.

A distinctive feature on a mature *Goniocheila* is the bulbous callus anteriorly situated on the body whorl adjacent to the inner lip (Figures 1G, 20). This bulbous callus assists in distinguishing *Goniocheila* from *Drepanocheilus* and *Aporrhais*. Similar callosities are present in some other genera of aporrhaid that are clearly distinct from *Goniocheila* and each other (e.g., *Anchura* Conrad, 1860, *Tessarolax* Gabb, 1864, *Pietteia* Cossmann, 1904, and *Platyptera* Conrad, 1855). In all cases the callosities appear functionally related to the position of the aporrhaid gastropod on the substrate and its mode of locomotion. Recent aporrhaid move forward in a "leap" that involves upward extension of the foot stalk followed by a forward topple of the animal and shell (Perron, 1978). In the Recent aporrhaid *Arrhoges occidentalis* (Beck, 1836) this "leap" results in speed greater than that of its

molluscan predators (Perron, 1978). Both during the animal's browse on the substrate and at a landing from a forward topple, the callus on the body whorl elevated the anterior end of the shell. With the anterior elevated, the animal would have been both ready to browse and able to recover more rapidly from its forward topple and more quickly take its next leap.

Abbreviations: The following institutional abbreviations are used: LACM = Natural History Museum of Los Angeles County, Malacology; LACMIP = Natural History Museum of Los Angeles County, Invertebrate Paleontology; NHM = The Natural History Museum (Great Britain); PRI = Paleontology Research Institute; TU = Tulane University; UF = Florida Museum of Natural History; USNM = United States National Museum of Natural History.

SYSTEMATIC PALEONTOLOGY

Placement of Aporrhaidae follows that of Ponder & Warén (1988).

Phylum MOLLUSCA Linnaeus, 1758

Class GASTROPODA Cuvier, 1797

Superorder CAENOGASTROPODA Cox, 1960

Order NEOTAENIOGLOSSA Haller, 1888

Superfamily STROMBACEA Rafinesque, 1815

Family APORRHAIDAE Gray, 1850

Genus GONIOCHEILA Gabb, 1868

Alipes Conrad 1865, p. 31 (non Imhoff, 1854, Myriopoda).
Goniocheila Gabb 1868, p. 144.

Type species: *Alipes liratus* (Conrad) (= *Chenopus liratus* Conrad, 1848), by subsequent designation, Cossmann (1904). Oligocene, Byram Formation, Mississippi.

Diagnosis: Small aporrhaid with outer lip triangulate expanded, extended into distal posterior labral digitation and having initially appressed apical digitation; distal lip margin callused. Whorls with two or three strong cords that extend onto the wing; posterior cord at angulate shoulder of mature whorls and extended onto posterior labral digitation; mature whorls noded at cords. Rostrum short and curved. Inner lip callused and with additional adjacent bulbous callus anterior to the posterior cord.

Discussion: *Goniocheila* has been repeatedly linked to the aporrhaid supraspecific taxa, *Aporrhais*, *Arrhoges* Gabb, 1868, and *Drepanocheilus*. Gabb (1868) proposed *Goniocheila* as a subgenus of *Aporrhais* and included in it *A. (G.) lirata* and "*A. (G.) sowerbyi* Sby. = *A. Parkinsonii* Sby." (Gabb, 1868:144). Gabb (1868) reproduced Conrad's figures of *G. lirata* which overemphasize the axial and under-represent the spiral sculpture. Figures in

MacNeil & Dockery (1984: pl. 28, figs. 11, 12) are more useful for recognizing characteristics of *Goniocheila* and of its type species *G. lirata*.

Gabb perhaps included “*A.*” *sowerbii* in *Goniocheila* on the basis of figures 1–5 of pl. 349 of Sowerby (1822). Both Fleming (1828) and Mantell (1829) recognized that these figures, labeled *Rostellaria parkinsoni* Mantell, were not that species, and each provided the name *Rostellaria sowerbii*. Fleming (1828:360) referred to figures 1 and 5 at the end of his brief species description; Mantell (1829:203) in a footnote, without description, provided the new name for figures 1, 3, 4. The specimen for fig. 4 of Sowerby, 1822: pl. 349 (NHM G.61992) was selected by Wrigley (1938) as lectotype for “*Aporrhais*” *sowerbii* (Mantell), but a lectotype does not seem to have been selected for “*R.*” *sowerbii* Fleming. Fleming’s (1828) inclusion in his *Rostellaria sowerbii* of only figures 1 and 5 of Sowerby’s plate 349 makes impossible designation of the lectotype of “*A.*” *sowerbii* of Mantell as lectotype of “*A.*” *sowerbii* (Fleming). Figure 5, based on a specimen from Folkstone, lacks features described by Fleming, and we here designate the specimen for figure 1, NHM 43750, as lectotype of *Rostellaria sowerbii* Fleming, 1828. The specimen came from “Maidenhead, between Bray and Windsor;” (Sowerby, 1822). According to Wrigley (1938), it was from the London Clay Basement Bed, which is either latest Paleocene (Berggren et al., 1985) or earliest Eocene (Curry, 1992). Wrigley included Sowerby’s figure 1 in the synonymy of *Aporrhais triangulata* Gardner, 1884, which was based on specimens from the Oldhaven beds of Paleocene, Thanetian age. The specimen chosen as lectotype of “*Aporrhais*” *sowerbii* (Mantell) was from the upper London Clay (Wrigley, 1938) and is of Eocene, Ypresian age.

Wrigley (1938) considered “*A.*” *sowerbii* (Mantell) and “*A.*” *triangulata*, despite their similarities, to belong to two different lineages, with “*A.*” *triangulata* (in which he included Sowerby’s figure 1) an end member of one, and “*A.*” *sowerbii* (Mantell) derived from “*Aporrhais*” *clarendonensis* (and evolving into “*Aporrhais*” *speciosa* [Schlotheim]) a member of the other. Illustrations of “*A.*” *triangulata* ? = “*A.*” *sowerbii* (Fleming) are similar to *Drepanocheilus perveta* (Stanton, 1920) of Paleocene age from the Cannon Ball Member of the Fort Union Formation of North and South Dakota. Both “*A.*” *triangulata* and *D. perveta* are similar to species of *Goniocheila* in overall shape, although in both the outer lip is more strongly embayed near the middle strong spiral than in *Goniocheila*. The anterior lip angulation is a feature noted by Gabb 1868, as characteristic of *Goniocheila*. “*Aporrhais*” *sowerbii* (Mantell) differs from the North American Oligocene species of *Goniocheila* in its longer straighter anterior rostrum, much broader and very shallow anterior sinus, and higher spire with more persistent *Drepanocheilus*-like arched axial ribbing. Wrigley (1938) considered “*A.*” *sowerbii* (Mantell) congeneric with 10

other Paleogene species including “*A.*” *speciosa* (Schlotheim, 1820). Some of Wrigley’s (1938) figures give indications of developing an anterior labral digitation.

As Gabb (1868) indicated, the shell of *Goniocheila* resembles that of *Aporrhais* in having an angulate shoulder and a second weaker, more anterior angulation, both of which are commonly noded. The angulations coincide with major cords. The apical digitation is short and adnate to the spire in geologically older species (*G. menthafon-tis*), becoming longer and free at its tip in geologically younger species (*G. wilsoni*). The distal margin of the outer lip is slightly convex to straight, and thickened between the posterior labral digitation and the anterior strong cord, at which the margin is subangulate. The posterior labral digitation is grooved interiorly, and at the anterior cord is a short, faint interior groove. The anterior sinus bordering the rostrum is narrow in *Goniocheila* and much wider in *Aporrhais* and in the Paleogene forms illustrated by Wrigley.

The body whorl of *Drepanocheilus* is also angulate at the shoulder and at least subangulate anteriorly at a strong cord. *Aporrhais* s.s. has at least one additional labral digitation at the anterior angulation. Both *Aporrhais* and *Goniocheila* develop posterior digitations, *Aporrhais* in the Cretaceous (Sohl, 1967), and *Goniocheila* in the Oligocene. MacNeil (in MacNeil & Dockery, 1984) argued that *Arrhoges* did not differ from *Goniocheila*, but Table 1 shows *Goniocheila* and *Arrhoges* to differ on two-thirds (four-fifths according to Table 2) of their characteristics, and shows *Arrhoges* to be more similar to *Latiala* Sohl, 1960.

Table 1 lists morphologic characteristics of the four genera: *Aporrhais*, *Arrhoges*, *Drepanocheilus*, and *Goniocheila*. This list of characteristics is modified from Roy (1994, 1996) to be pertinent to these four genera. Figure 1 illustrates some aporrhaid shell descriptive terms (see also Popenoe, 1983: fig. 2). The expanded outer lip (apertural process of Roy 1994, 1996) is commonly referred to as a wing. Wing shape is variable within species (e.g., the wing of *A. pespelecani* (Linnaeus, 1758) with variation in length and number of digitations), and wing form is difficult to describe succinctly. In *Drepanocheilus* and *Goniocheila* it is somewhat triangular to crescentic. *Arrhoges* has a more quadrate wing, and that of *Aporrhais* is splayed. The two directions on the wing, axial (height) and spiral (width), give proportional information. On Table 1, height is “tall” or “short” and width is “broad” or “narrow.” Some species of *Aporrhais* (e.g., *Aporrhais serresiana* Michaud, 1828, Recent, Mediterranean to Iceland; *Aporrhais uttingeriana* [Risso, 1826], Pliocene, Europe) have long digitations, but several European Tertiary species have digitations of moderate length. Roy (1994) considered *Aporrhais* to have a multidigitate (more than two digitations) wing, a criterion that would exclude from it most of the early Tertiary forms discussed by Gardner

Table 1
Morphologic characteristics of four aporrhaid genera.

Morphologic characters	<i>Aporrhais</i>	<i>Arrhoges</i>	<i>Drepanocheilus</i>	<i>Goniocheila</i>
* 1. Shell shape: elongate//short and stout	elongate	elongate	both	short and stout
* 2. Relative spire height: high//moderate (= height of body whorl)	high	high	high	moderate
3. Sides of immature whorls: angular//rounded	both	rounded	rounded	both
4. Sides of mature whorls: angular//rounded	angular	rounded	angular	angular
* 5. Rostrum: long//short (< half length of body whorl)	both	short	both	short
* 6. Rostrum: straight//curved	curved	straight	?straight	both
* 7. Rostrum width: narrow//broad	narrow	broad	narrow	narrow
* 8. Apical digitation adnate to spire: present//absent	partly	absent	if present	partly
9. Apical digitation: long//short//absent	long/short	absent	short/absent	short
*10. Apical digitation extending beyond spire: yes//no//absent	yes/no	absent	no	no
*11. Callus on spire: present//absent	present	absent	some	some
12. Callus knob on base near aperture: lumpy//present//absent	present	absent	present	lumpy
13. Callus knob on outer lip edge: present//absent	absent	absent	absent	present
14. Apertural expansion (wing): equant/inequant	equant	equant	inequant	equant
*15. Apertural expansion (wing): single//multidigitate	multidigitate	single	single	single
16. Apertural expansion (wing): tall//short	tall	tall	short	tall
*17. Apertural expansion (wing): broad//narrow	broad	broad	broad	broad
18. Distal margin of wing: convex//concave//straight	concave/straight	convex	convex	convex
*19. Number of digits: 1//1 or 2//2 or more	2 or more	1	1	1
20. Wing interior channeled opposite digitations	yes	no	yes	yes
21. Number of wing interior channels	2 or more	0	1	1
*22. Length of labral digitations: long//moderate//short	long	short	moderate	moderate
*23. Wing digitations: lobed//spiny//both	spiny	lobed	spiny	spiny
*24. Webb between digitations: present//absent	present	absent	absent	absent
*25. Concave posterior margin of wing	yes	no?	yes	yes
*26. Sculpture: strong//moderate//fine//absent	strong	moderate	moderate	strong
27. Dominant sculpture type on mature whorls: axial//spiral	spiral	axial	spiral	spiral
*28. Spiral body cords extending to wing: present//absent	present	absent	present	present
*29. Row of shoulder nodes: present//absent	present	absent	either	present
*30. Axial nodes: strong//weak//absent	strong	absent	weak	strong
31. Two-four strong cords on whorl: present//absent	present	absent	present	present
Similarity to <i>Goniocheila</i>	0.64	0.32	0.77	1.00
Similarity to <i>Aporrhais</i>	1.00	0.26	0.55	0.64
Similarity to <i>Arrhoges</i>	0.26	1.00	0.45	0.32
Similarity to <i>Drepanocheilus</i>	0.55	0.45	1.00	0.77

Morphologic characters * from lists of Roy, 1994, 1996.

(1884) and Wrigley (1938). The presence of two to four strong cords on the whorls (Figure 1H) is here considered significant as these cords commonly extend across the wing and onto digitations, suggesting that the cords reflect persistent features of the mantle.

Paleocene and Eocene species of *Drepanocheilus* are in general stouter and have thicker callus deposits about the aperture (e.g., *Drepanocheilus pervata* [Stanton, 1920], "A." *triangulatus* [Gardner, 1884] ? = "A." *sowerbii* [Fleming]) than do the more typical Cretaceous species. Species of Oligocene age referred to *Drepanocheilus* differ in several respects from typical *Drepanocheilus*. They are stouter, have a taller wing, have stronger nodes on the body whorl, usually have a posterior digitation adnate to the spire, some have a long posterior labral digitation, and some have an anterior labral digitation.

Most resemble more typical *Drepanocheilus* in the sculpture of the spire.

Cossmann (1904) included *Goniocheila* in *Arrhoges* (along with representatives of *Drepanocheilus*, *Latiala*, *Goniocheila*, and *Aporrhais*), but *Arrhoges* and *Latiala* lack the strong cords of *Goniocheila*, *Drepanocheilus*, and *Aporrhais*. The rostrum of *Goniocheila* is more bent and narrower than that of *Arrhoges*, and *Arrhoges* has a shallow and very broad anterior sinus. Sculpture exposed on early whorls of the spire of *Goniocheila*, *Arrhoges*, and *Drepanocheilus* consists of spiral cordlets and arched axial ribs, but anterior to the periphery, the sculpture of *Drepanocheilus*, *Aporrhais*, and *Goniocheila* is dominated by two or three strong cords, whereas whorls of *Arrhoges* are covered by many, more nearly uniform cordlets. Wrigley (1938) noted that *Aporrhais sowerbii* form

Table 2

Comparison of four aporrhaid genera omitting morphologic characteristics of wing and its digitations. Limiting characteristics to 16 characteristics (characteristics 1–7, 11–13, 26–31 of Table 1) makes *Goniocheila* and *Aporrhais* most similar.

Similarity to	<i>Aporrhais</i>	<i>Arrhoges</i>	<i>Drepanocheilus</i>	<i>Goniocheila</i>
<i>Goniocheila</i>	0.75	0.19	0.69	1.00
<i>Aporrhais</i>	1.00	0.31	0.81	0.75
<i>Arrhoges</i>	0.31	1.00	0.50	0.19
<i>Drepanocheilus</i>	0.81	0.50	1.00	0.69

clarendonensis Wrigley, 1938, of early Ypresian age, was an *Arrhoges*. The species resembles an *Arrhoges* in having spiral cordlets of roughly equal strength with barely stronger spiral cords positioned as in *Drepanocheilus*, *Aporrhais*, and *Goniocheila* (in which it was included by MacNeil (in MacNeil & Dockery, 1984). Unfortunately, all specimens of "A." *clarendonensis* from Clarendon in the LACMIP collection (Figures 6, 7) have a broken outer lip, but Gardner's (1884) illustration of the wing (pl. 17, figs. 5, 6) shows it, unlike that of *Arrhoges*, considerably expanded anteriorly.

Wrigley suggested that the better represented of his two lineages began with "A." *clarendonensis*, led into "Aporrhais" *speciosa*, and evolved toward a multidigitate aperture and typical *Aporrhais*. MacNeil (in MacNeil & Dockery, 1984) indicated that *Aporrhais* arose from *Goniocheila* and that *Aporrhais pespelecani* was aberrant. He did not mention that specimens resembling *Aporrhais* with angulated whorls, noded carinae, and more than two wing digitations are present in the Cretaceous (i.e., *Aporrhais drachuki* Saul, 1998, southern California, Turonian; *A. biangulata* [Meek & Hayden, 1856], Wyoming and Montana, Campanian; *Aporrhais* n. sp., Sohl, 1967, Alabama, early Campanian). MacNeil (in MacNeil & Dockery, 1984) suggested that *Aporrhais gracilis* Aldrich, 1886, from the Gulf Coast Eocene was more similar to early Eocene species figured by Wrigley (1938) (but did not specify which species) than are the southern U.S. species *G. lirata* and *G. menthafontis*. *Aporrhais gracilis* (in Harris, 1899) has a wing doubly digitated on its distal margin, and a whorl profile on the spire that is angulated, as are those of *Aporrhais pespelecani*. Among Wrigley's figures, *A. gracilis* is most similar to "A." *londiniensis* Wrigley, 1938, but differs in having the angulated whorl on the spire rather than the rounded whorl with sculpture resembling that of *Drepanocheilus* as in the English Paleocene and Eocene species (Wrigley, 1938).

Protoconchs, early sculpture, strong spiral cords, and wing shape of *Goniocheila*, *Drepanocheilus*, and some "A." *speciosa* are similar. If multidigitate *Aporrhais* ap-

pearing in the Late Cretaceous is monophyletic, rather than consisting of a series of iterative offshoots from a unidigitate lineage, it has greater antiquity than *Goniocheila* (unknown before Oligocene) and *Arrhoges* s.s. (Kollmann & Peel, 1983 recognize *Arrhoges* (*Latiala*) *palaeocaenica* Rosenkrantz, 1970, Paleocene, Greenland, as *Arrhoges* s.s. rather than as a *Latiala* Sohl, 1960; *Latiala*, proposed as a subgenus of *Arrhoges*, is known as early as the Aptian [Saul, 1998]).

In Table 1, *Goniocheila* is limited to characteristics evinced by *G. lirata*, *G. menthafontis*, and *G. wilsoni*. In these, the wing is, as described by Gabb, somewhat bangular with the posterior angle produced into a digitate process, and the anterior not produced, but having on its inner anterior face a faint, very short groove. Additionally, the distal wing margin is nearly straight to somewhat convex and heavily callused from the posterior digitation to the position of the middle cord. In *Aporrhais* this cord extends onto a labral digitation, and *Aporrhais* is largely defined by characteristics of *A. pespelecani* (Figures 2, 3, 8) and *A. serrisiana*. Characteristics of *Drepanocheilus* are those of the type species *D. evansi* Cossmann, 1904, (= *Rostellaria americana* Evans & Shumard, 1857 non d'Orbigny, 1842) (Figures 4, 5). *Arrhoges* is exemplified by its type species *A. occidentalis* (Figures 9–11).

Fifteen or nearly half of the characteristics of Table 1 pertain to the wing. Eight of these characteristics pertain to the digitations of the wing, which are probably variable. Digitations vary as to number and length from specimen to specimen within Recent species of *Aporrhais*, and the apical digitation arises through time in *Drepanocheilus*, *Aporrhais*, and *Goniocheila*. The wing is often missing from fossils, but as seen from Table 2, which lists comparisons of the four genera with the wing characteristics omitted, the genera can be distinguished upon the remaining characteristics. Without the wing characters, *Drepanocheilus*, *Aporrhais*, and *Goniocheila* are significantly more similar to each other than to *Arrhoges*, but *Goniocheila* is more similar to *Aporrhais* than to *Drepanocheilus*.

The three species of *Goniocheila* are a distinctive and compact group, showing far less morphologic diversity than has been ascribed to "A." *speciosa* s.l. Roy (1994) showed *Goniocheila* as present in the Turonian, based upon *Aporrhais* (*Goniocheila*) *castorensis* Whitfield, 1877, from the Benton Shale in the Black Hills, but the inadequately figured holotype (Whitfield, 1880: pl. 12, fig. 1; Stanton, 1893: pl. 31, fig. 1) lacks characteristics of *Goniocheila*, and appears closer to *Drepanocheilus*. Abbass (1967) referred an incomplete aporrhaid specimen from the Eocene of Egypt questionably to *Goniocheila orientalis*, but the fine arcuate ribbing of the spire is more suggestive of *Drepanocheilus* than of *Goniocheila*. At present, no specimens of earlier than Oligocene age can be assigned to *Goniocheila*, and the genus ranges from early to latest Oligocene or early Miocene age.

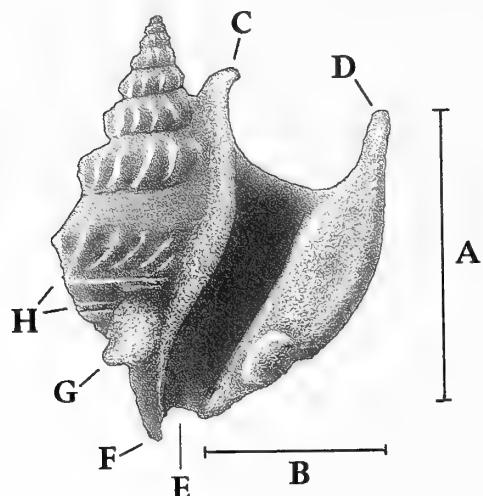


Figure 1. Some descriptive terms applied to *Goniocheila*. A = wing (expanded outer lip) height. B = wing (expanded outer lip) breadth. C = apical digitation. D = posterior labral digitation. E = anterior sinus. F = rostrum. G = bulbous callus on body whorl. H = strong spiral cords on anterior whorl slope.

Goniocheila wilsoni Saul & Petit, sp. nov.

(Figures 1, 12–22)

Aporrhais n. sp. Carter, Gallager, Valone, & Rossbach, 1988, p. 82, pl. 7, fig. 54.

Diagnosis: A *Goniocheila* having a well developed posterior digitation curling away from spire toward posterior lateral labral digitation and a deep, narrow anterior sinus immediately adjacent to the short rostrum. Whorl profile well angulated and noded especially on body whorl.

Description: Shell medium sized, fusiform with expanded outer lip, spire slightly less than half of shell height. Protoconch of three polished, globular whorls. Earliest sculpture on teleoconch of spiral ridges for about one half whorl, then fine, concavely arcuate axial ribs added. Ribs faint and moderately crowded, quickly becoming stronger, enlarged at shoulder, and reduced to half as many on second teleoconch whorl; following whorls with about 14 axial ribs per whorl. Whorl profile of first two post protoconch whorls convex, axial on next four spire whorls

weak near posterior suture and strongest at periphery, weakening toward anterior suture. Strength of axials at periphery producing concave whorl profile near posterior suture, subangulate at periphery, and convex between shoulder and anterior suture. Shoulder closer to posterior suture on earlier whorls becoming just below mid whorl on penultimate whorl. Ribs abruptly shorter on last whorl becoming nodes on peripheral cord. Cord extending to end of tip of wing. Two anterior cords present on body whorl. Spiral cordlets overall; on body whorl cordlets intermediate to anterior cords strengthen; three cordlets on whorl base nearly as strong as intermediate cordlets. Outer lip expanded into broad, somewhat crescentic wing with broadened distal edge posteriorly pointed by labral digitation, concave posterior edge, and curving posterior digitation adnate to two whorls but pointed away from spire at its tip. Two strong calluses developed, one at anterior end distal wing edge, other opposite on base of body whorl. Aperture elongate, sinused anteriorly and posteriorly with nearly parallel lips, angled about 25° to axis. Rostrum short, nearly straight, narrow with closely adjacent deep anterior sinus.

Holotype: USNM catalogue number 508381.

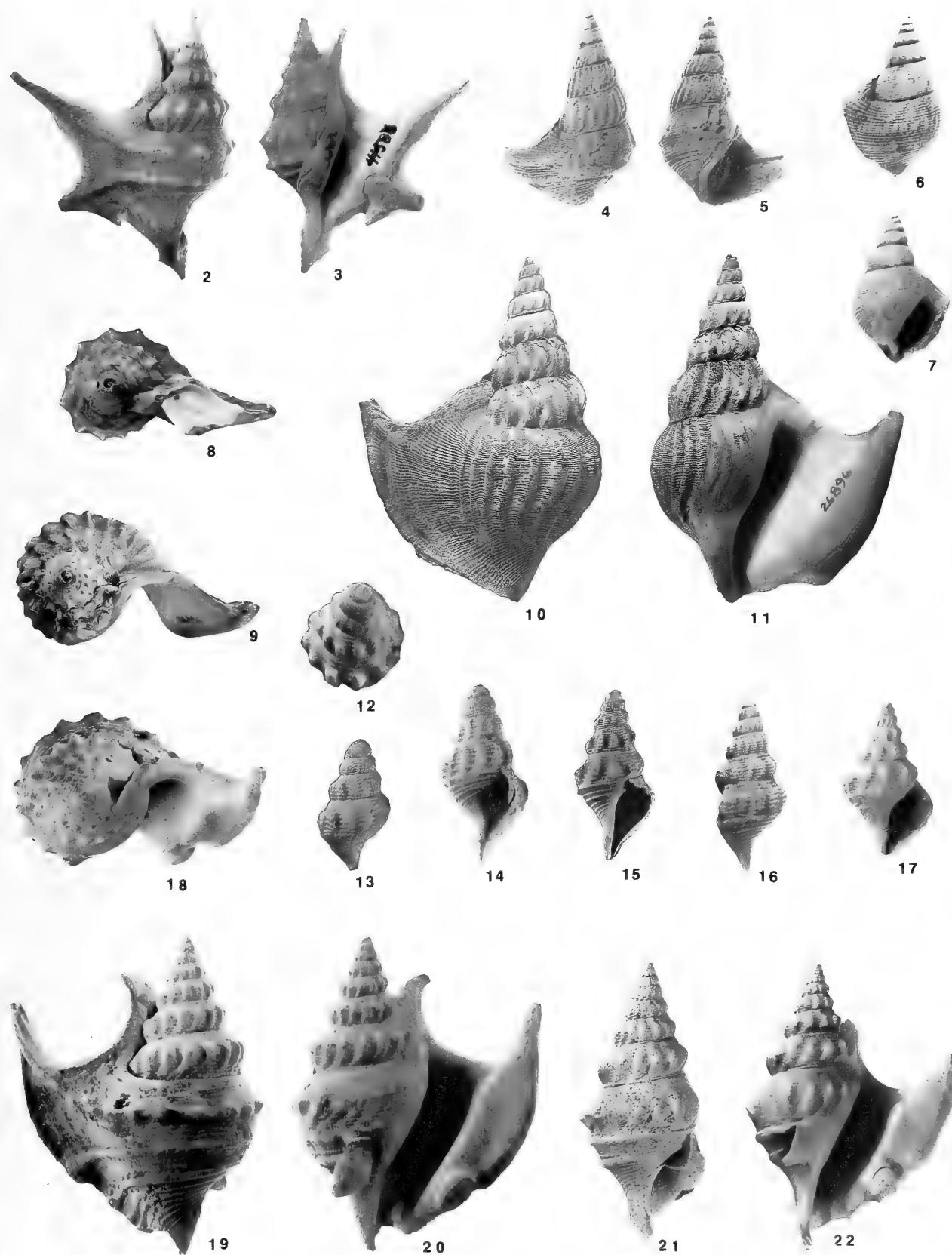
Type locality: "Silverdale Beds." Silverdale, North Carolina = Tulane loc. TU 866 (marl pit on north side of Webb Creek and east side of unnumbered county road, Silverdale, Onslow County, North Carolina [Vermeij & Vokes, 1997]). Coll. Dick & Liz Petit, 1968–1970. Belgrave Formation, Haywood Landing Member. Latest Oligocene

Paratypes: LACMIP catalogue numbers 12636–12642, PRI catalogue number 49395, UF catalogue number 102475, all from TU loc. 866.

Dimensions of holotype: Height 28.2 mm, diameter 21.8 mm. (last whorl and wing); diameter last whorl at 90° to wing 12.5 mm; height penultimate whorl 4.4 mm; diameter penultimate whorl 10 mm.

Height of paratypes: LACMIP 12636, 24.6 mm; LACMIP 12637, 3.8 mm; LACMIP 12638, 5.2 mm; LACMIP 12639, 7.0 mm; LACMIP 12640, 7.6 mm; LACMIP 12641, 9.5 mm; PRI 49395, 24.8 mm.

Figures 2–22. Figures 2–11, 19–22 coated with ammonium chloride. Figures 2, 3, 8, *Aporrhais pespelecani* (Linnaeus, 1758), hypotypes, from Mediterranean Sea, $\times 1$; Figures 2, 3. LACMIP 149737. Figure 2. Back. Figure 3. Aperture. Figure 8. LACMIP 149738, apical view. Figures 4, 5. *Drepanocheilus evansi* Cossmann, 1904, hypotype, LACMIP 12643, from LACMIP loc. 25073, $\times 1.5$. Figures 6, 7. "*Aporrhais*" *clarendonensis* Wrigley, 1938, hypotype, LACMIP 12644, from LACMIP loc. 28428, $\times 2$. Figures 9–11. *Arrhoges occidentalis* (Beck, 1836), hypotype, LACMIP 152351, off Scantari Bank, Newfoundland, Canada at 250 fathoms, $\times 1$; Figure 9. Apical view. Figure 10. Back. Figure 11. Aperture. Figures 12–22, *Goniocheila wilsoni* Saul & Petit, sp. nov. from TU loc. 866. Figures 12, 13. Paratype, LACMIP 12637. Figure 12. Protoconch, $\times 8$. Figure 13. Back, $\times 6$. Figure 14. Paratype, LACMIP 12638, aperture, $\times 6$. Figure 15. Paratype, LACMIP 12640, aperture, $\times 4$. Figure 16. Paratype, LACMIP 12639, labral side, $\times 4.4$. Figure 17. Paratype, LACMIP 12641, $\times 3$. Figures 18–20. Holotype, USNM 508381, $\times 2$. Figure 18. Apical view. Figure 19. Back. Figure 20. Mature aperture. Figure 21. Paratype, PRI 49395, ablbral side, $\times 2$. Figure 22. Paratype, LACMIP 12636, maturing aperture, $\times 2$.



Discussion: The early *Drepanocheilus*-like spire sculpture is confined to about two whorls after which the axial coarsen, fade toward the sutures, especially the posterior suture, and strengthen on the shoulder. A series of specimens (Figures 13–16) shows that the strong anterior cords visible on the last whorl begin to be present on immature specimens at a height of 7 mm and are well developed at a height of 7.6 mm. The distal edge of the outer lip is considerably thickened between the labral digitation and the labral end of the more anterior cord. The wing is first thin and distally forward-facing. This forward-facing lip margin is slightly grooved and notched at the two strong cords of the exterior. Then the wing is thickened especially toward the distal margin to form a narrow parallel-sided aperture with a thick, broad, forward-facing outer lip with a callus knob adjacent to the two notches. The anterior grooves interior to the cords are filled, but the groove along the labral digitation remains, as does the groove along the posterior digitation. Both of these grooves face more laterally than ventrally, and the labral digitation groove is nearly hidden in apertural view by the distal labral callus. The anterior sinus of *G. wilsoni* is unusually narrow and deep for an aporhaid.

Goniocheila wilsoni has a more angulate whorl profile than either *G. menthafontis* or *G. lirata*. It has stronger and fewer axial ribs on the spire, a shorter spire, and a longer posterior digitation which, unlike that of the two geologically older species, curls away from the spire and points toward the posterior lateral labral digitation. In its strongly noded peripheral cord *G. wilsoni* is more similar to *G. menthafontis* than to *G. lirata*.

Etymology: The species is named for Druid Wilson of Lake Wales, Florida, stratigrapher and paleontologist, formerly of the Paleontology and Stratigraphy Branch of the U.S. Geological Survey, in appreciation for his many contributions to our knowledge of Tertiary Mollusca.

Acknowledgments. Lindsey T. Groves (LACMIP) provided access to collections and obtained some hard-to-find literature. Paul Jeffrey (NHM) kindly searched for, found the specimen figured by Sowerby (1822: pl. 349, fig. 1), and provided to us its Natural History Museum number. Photos for Figures 8–11 were taken by Takeo Susuki, and photos for Figures 12, 13, and 15 were provided by Richard L. Squires. We thank the reviewers and editor for helping us make this a more readable paper.

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APPENDIX

Locality descriptions for fossils illustrated.

- 866 TU: "Silverdale Beds." Silverdale, North Carolina (marl pit on north side of Webb Creek and east side of unnumbered county road, Silver-

dale, Onslow County, North Carolina. Coll. Dick & Liz Petit, 1968–1970. Belgrade Formation, Haywood Landing Member. latest OLIGOGENE, Chattian.

- 25073 LACMIP [= UCLA loc. 5073]: limey concretions in shale exposed on north bank Grand River about 762 m (2500') S, 427 m (1400') E of NW cor. sec. 24, T. 21 N, R. 24 E, Bullhead Quad. (USGS 1956), Corson County, South Dakota. Coll: T. Susuki, 1963. Fox Hills Formation, Trail City Member, *Protocardia* zone. CRETACEOUS, Maastrichtian.

- 28428 LACMIP: Clarendon, Wiltshire, England. Coll.? & id. Arthur Wrigley—sent by Wrigley to UCLA (exUCLA 11439). London Clay. EO-CENE, Ypresian.

Varicorbula (Bivalvia: Corbulidae) of the Western Atlantic: Taxonomy, Anatomy, Life Habits, and Distribution

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Abstract. The taxonomy, anatomy, life habits, and distribution of the three western Atlantic species of *Varicorbula* are discussed. *Varicorbula disparilis* (d'Orbigny, 1842) is recognized as valid and widely distributed, based on museum material (including lectotype designation), literature, and new collections (by Shipek grab and otter trawl) from the westernmost Florida Keys. *Corbula* [or *Notocorbula*] *operculata* Philippi, 1848, the most often applied name to this form, is considered a *nomen dubium* in the absence of locatable type material; *C. limatula* (Conrad, 1846) is confirmed as a synonym by examination of type specimens. Anatomy is largely congruent with that previously reported for members of *Varicorbula* and *Corbula*. The known geographic range of *V. disparilis* includes North and South Carolina, Georgia, eastern Florida, through the Gulf of Mexico, the Bahamas, and Yucatan, with unverified records from Virginia and several West Indian islands; it is associated with sand or mud habitats from relatively shallow depths to below 1400 m. Attached epifaunal mollusks associated with the Florida Keys samples suggest that this species lives epibenthically in densities of nearly 400 individuals/m². Two other Recent western Atlantic members of *Varicorbula* are recognized as valid, both of which had been previously synonymized by various authors with *V. disparilis*/*limatula*/*operculata*. Provisionally maintained as distinct species based on shell characters are: *C. krebsiana* C. B. Adams, 1852 (Jamaica and Puerto Rico only), and *C. philippii* E. A. Smith, 1885 (Bermuda, North Carolina, Florida, Texas, Yucatan, the Caribbean, and Brazil). A revised diagnosis of the genus *Varicorbula* is presented, based on the type species, *V. gibba* (Olivi, 1792), and new data for the species studied here. In the context of existing taxonomic definitions, *Varicorbula* is properly placed in the subfamily Caestocorbulinae (rather than Corbulinae or Caryocorbulinae), a subfamily otherwise known only from the Cretaceous and Eocene.

"Recent specimens of *Varicorbula* of the western Atlantic represent a taxonomic quandary..."

—L. C. Anderson, 1996: 21.

INTRODUCTION

Varicorbula disparilis (d'Orbigny, 1842) [as *Corbula*] was originally described from Guadeloupe. This species has been most frequently called *V.* [or *Corbula* or *Notocorbula*] *operculata* (Philippi, 1848), described from the Caribbean island of St. Thomas. Earlier literature finds it cited as *C. limatula* Conrad, 1846, described from the Gulf of Mexico off the western coast of Florida. Although it is often listed from offshore dredge samples (Bush, 1885a, b; Dall, 1889; Abbott, 1954, 1974; Warmke & Abbott, 1961; Weber, 1961; Odé, 1971, 1976; Waller, 1973; Porter, 1974; Porter & Wolfe, 1971; Treece, 1979; Calnan & Littleton, 1985a, b; Jensen & Harasewych, 1986; Vittor, 1998), it is usually collected only as empty

shells (Abbott, 1954, 1974; Merrill et al., 1978; Calnan & Littleton, 1985a, b; Lyons, 1989, personal observation) and nothing is known of its anatomy or biology.

During a research cruise to the Marquesas Keys and Dry Tortugas in the western Florida Keys, fortuitous and abundant living collections of this rarely live-collected myoidean clam were obtained by Shipek grab and otter trawl. This provided an opportunity to study its morphology, to make comparisons with the few existing non-conchological data recorded for the family (Yonge, 1946; Morton, 1990), to evaluate other western Atlantic species, and to re-examine distinguishing characters of this genus. In addition, the samples allowed unique observations on population structure and life habits.

MATERIALS AND METHODS

This study is part of an ongoing investigation of marine molluscan biodiversity in the Florida Keys (Bieler &

Table 1
R/V *BELLOWS* stations in which *Varicorbula disparilis* specimens were collected.

Sta. no.	Date (1997)	Location	Coordinates	Depth (m)	Gear
FK-075	22 April	NNW or Marquesas Keys; mud	24°44'05"N, 82°14'24"W	21	Shipek grab
FK-077	22 April	NNW of Marquesas Keys	24°45'00"N, 82°15'00"W	21	Shipek grab
FK-078	22 April	due E of New Ground, NW of Marquesas Keys	24°40'40"N, 82°16'46"W	12	Shipek grab
FK-082	22 April	NNW of New Ground, between Marquesas Keys and Dry Tortugas	24°48'17"N, 82°28'42"W	27	Shipek grab
FK-084	22 April	N of Rebecca Shoal, between Marquesas Keys and Dry Tortugas	24°44'24"N, 82°37'24"W	29	Shipek grab
FK-085	22 April	NNW of East Key, Dry Tortugas; thick clay	24°49'12"N, 82°43'54"W	33	Shipek grab
FK-096	24 April	due S of Dry Tortugas	24°19'48"N, 82°54'06"W	223	Shipek grab
FK-098	24 April	due S of Dry Tortugas	24°24'48"N, 82°52'36"W	60	Shipek grab
FK-100	25 April	S of East Key, Dry Tortugas	24°34'18"N, 82°46'54"W	31	Shipek grab
FK-104	25 April	NNE of New Ground, between Marquesas Keys and Dry Tortugas	24°47'18"N, 82°18'18"W	23	Shipek grab
FK-106	25 April	NNE of New Ground, between Marquesas Keys and Dry Tortugas	24°47'18"N, 82°18'18"W to 24°48'12"N, 82°19'06"W	23–24	25' otter trawl (~1 hr bottom time)

Mikkelsen, 1999), formally initiated by the authors in 1994. Samples were collected during a four-day research cruise to the Dry Tortugas, the westernmost Florida Keys, aboard R/V *BELLOWS* (Florida Institute of Oceanography, St. Petersburg, Florida). Thirty-five living specimens of *Varicorbula disparilis* were obtained in one Shipek grab sample (sta. FK-104, see Table 1 for locality data for all cited stations). An immediately subsequent otter trawl sample (sta. FK-106) brought aboard another estimated 3200 specimens entangled within an elastic, grey fibrous mat covering the trawl's "tickle chain" (Figures 1, 2).

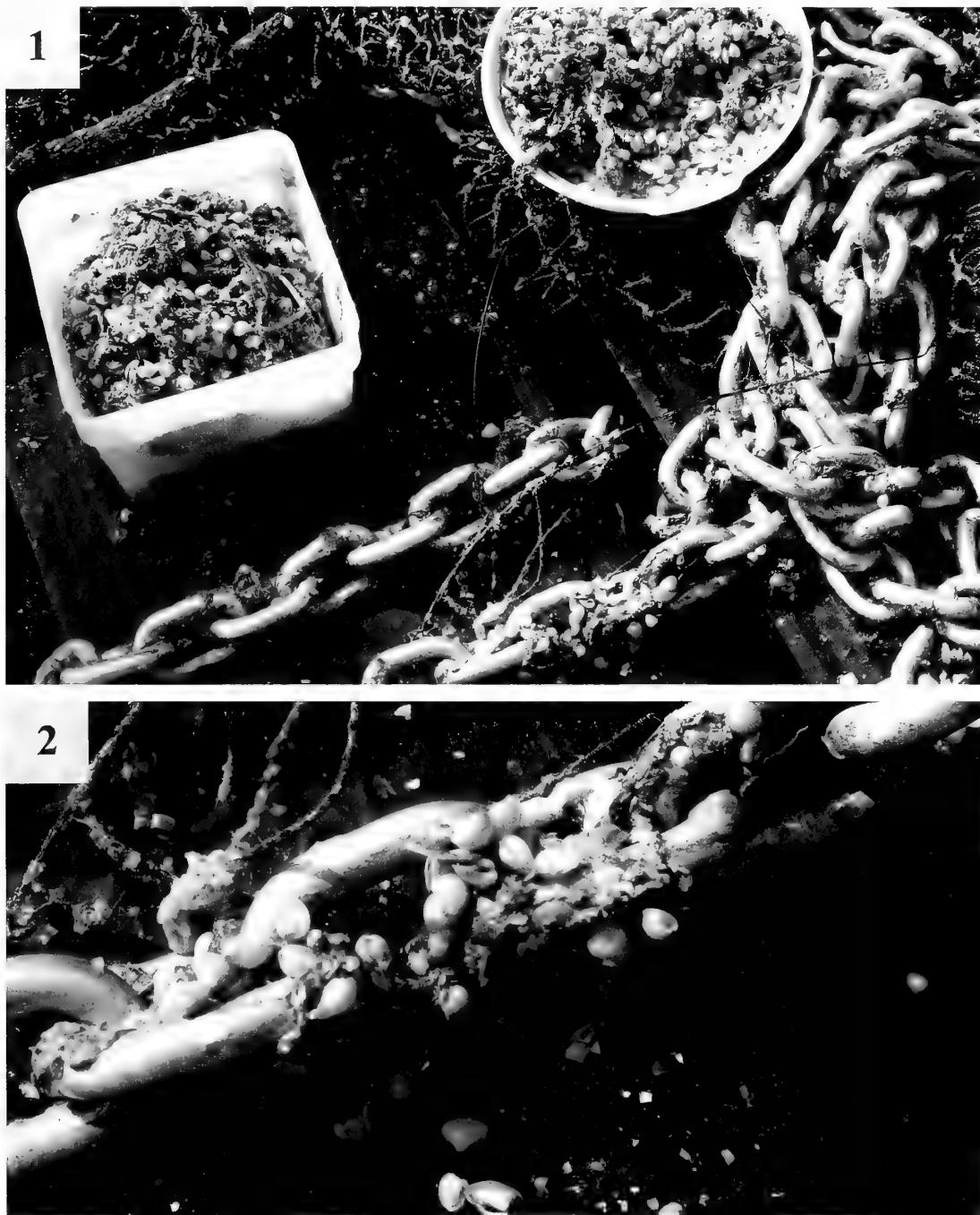
Living clams were hand separated from the Shipek grab sample, relaxed in aqueous magnesium sulfate, and fixed in 5% formalin (later transferred to 70% ethanol); the remainder was sieved through a 350 µm sieve to remove fine sediment, then dried. The trawl sample included the fibrous mat with the living clams; both were manually removed from the chain. While still aboard ship, the clams were hand separated from the mat, relaxed, fixed, and preserved as above; the mat fragments were preserved in 70% ethanol. Empty shells of *Varicorbula disparilis* were collected in other Shipek grab samples in the same general vicinity in the Gulf of Mexico (stas. FK-075 through 100).

For histological examination, shells were removed manually from formalin-fixed, ethanol-preserved specimens (sta. FK-106). The specimens were dehydrated through a graded ethanol series, followed by clearing in xylene substitute (Hemo-De®, Fischer Scientific, Pittsburgh, Pennsylvania), and embedding in paraffin (Paraplast X-tra®; Oxford Labware, St. Louis, Missouri). Complete 7-µm serial sections were produced for intact individuals in lateral or anteroposterior orientation, and

stained with hematoxylin/eosin. Histological sections and dried shells were photographed under light microscopy. For scanning electron micrography, dried shells and critical-point dried animals were mounted on stubs, coated with gold-palladium, and scanned on a Zeiss DSM-950 scanning electron microscope at AMNH.

Synonymies herein are restricted to original descriptions, significant taxonomic works, and descriptions and geographical records verifiable through published illustrations or museum lots. Cited repositories are: AMNH, American Museum of Natural History (New York); ANSP, Academy of Natural Sciences of Philadelphia; BMNH, The Natural History Museum (London); DMNH, Delaware Museum of Natural History (Wilmington); FMNH, Field Museum of Natural History (Chicago); HMNS, Houston Museum of Natural Science (Texas); MCZ, Museum of Comparative Zoology, Harvard University (Cambridge, Massachusetts); NCSM/IMS, North Carolina State Museum of Natural Sciences (Raleigh); SBMNH, Santa Barbara Museum of Natural History (California); UMMZ, University of Michigan, Museum of Zoology (Ann Arbor); USNM, National Museum of Natural History, Smithsonian Institution (Washington, D.C.).

Selected material examined: *Varicorbula disparilis* (d'Orbigny, 1842) (39 lots, 3088+ specimens): NORTH CAROLINA: SE of Cape Lookout, 34°24.3'N, 76°35.9'W, grab, 24 m, Duke University BLM Project #65818252, 13 August 1981, NCSM/IMS 9276 (6 alc.); R/V *OREGON* #6516, SE of New River Inlet, 34°17' to 34°16'N, 77°11' to 77°14'W, 13 fms (24 m), Porter!, 24–25 March 1967, NCSM-IMS 3008 (20+, some live collected). SOUTH CAROLINA: R/V *EASTWARD* sta. #11545, off Charleston, 32°41.8'N, 78°32.4'W, coarse sand, 50 m, H. J. Porter!, 16 March 1969, NCSM/IMS 2868 (20+) (Porter, 1975).



Figures 1, 2. *Varicorbula disparilis* entangled in byssal mat, as captured on the tickle chain of an otter trawl.

GEORGIA: R/V DAN MOORE, ESE of Savannah, Calico Scallop Grounds, 31°54'N, 79°49'W, modified tumbler dredge, 20–22 fms (37–40 m), sand, 22 January 1978, NCSM/IMS 7459 (1 alc., 53 dry). EASTERN FLORIDA: R/V GOSNOLD Cr. 222, sta. 273a, off Ft. Pierce, 27°34.0'N, 80°02.2'W, pipe dredge, 37 m, D. K. Young!, 28 February 1974, HBOM 064:01469 (7 + 260 valves, in alcohol); 10 nmi (18.5 km) off Ft. Pierce, St. Lucie County, 27°33.25'N, 80°03.2'W, dredged, 33 m, R. W. Virnstein!,

November 1977, DMNH 179615 (50+); R/V JOHNSON Cr. 045, Recol. sta. II, 25.4 km east of Ft. Pierce, St. Lucie County, 27°33.2'N, 80°03.2'W, recolonization tray experiment (uncovered compartment), 33 m, R. W. Virnstein!, 14 August 1977, HBOM 064:01908 (53, in alcohol); off Palm Beach, 50 fms (91.5 m), T. L. McGinty!, June 1940, FMNH 23497 (3); off Palm Beach County, 3 fms (5.5 m), Donovan!, July 1940, AMNH 232601 (4); Gulf Stream, out from Bounton [*err pro* Boynton Beach?],

Palm Beach County, 35–45 fms (64–82 m), F. Lyman!, 1940, FMNH 20352 (5); 7 ms south from Fowey Rocks Light, Dr. W. H. Rush!, ANSP 50908 (5 valves). FLORIDA KEYS: shell shop purchase, dredged, 50 m, E. S. Phillips Collection, SBMNH 55425 (5); off Alligator Reef Light, 600 ft (183 m), J. Moore! 1965, ANSP 312497 (20+ valves); north of Key West, 80–150 ft (24–46 m), September 1963, AMNH 144874 (1); Dry Tortugas, 60–45 fms, Dr. W. R. Taylor!, 1925, ANSP 141066 (17 valves). WESTERN FLORIDA (GULF OF MEXICO): Gulf of Mexico, Smith!, 1962, FMNH 151867 (2); Gulf of Mexico, J. Moore!, FMNH 223517 (ex FMNH 165115) (1); Gulf of Mexico, off Florida, deep water, ANSP 50909 (lectotype + 2 paralectotypes; see text); west of Boca Grande, dredged, 170 ft (52 m), coral rubble and clay, J. Moore!, AMNH 182093 (2); southwest of Anna Maria Island, dredged, 300–400 ft (91–122 m), J. Moore!, AMNH 107795 (1); southwest of Egmont Key, N. Heppeler!, 1971, DMNH 45248 (5); west of Egmont Key, 300 ft (91 m), J. Moore!, July 1964, ex Germer Collection, AMNH 273277 (14); southwest of John's Pass [St. Petersburg], 27 fms (49 m), Steger! 1965, ANSP 306297 (in part) (11); west of Anclote Key, 90–100 ft (27–30.5 m), J. Moore!, December 1967, AMNH 180242 (2); west of Bayport, 150 ft (46 m), J. Moore!, May 1963, ex Germer Collection, AMNH 273274 (13); 90 mi (145 km) west of Crystal River, dredged, 30 fms (55 m), J. Moore!, 1963, ex Feinberg Collection, AMNH 176008 (3); west of Cape San Blas, east edge of DeSoto Canyon, 100–300 fms (183–549 m), D. & R. Black!, 1971, AMNH 167213 (8); off Cape San Blas, 29°33.5'N, 84°38'W, 10 fms (18 m), H. Kritzler!, 22 January 1972, DMNH 50261 (5); off Panama City, 30°01.0'N, 86°20.0'W, M. Jones!, 08 April 1958, AMNH 145190 (1); off Destin, 14 fms (26 m), T. L. McGinty!, ANSP 25214 (50+ valves); off Destin, dredged, 15 fms (27.5 m), September 1940, ex Wisoff Collection, AMNH 120491 (6 + 1 valve). GULF OF MEXICO (OTHER STATES): Alabama, south of Mobile, 30°04'30"N, 88°36'W, 62–68 ft (19–21 m), D. R. Moore! 27 June 1960, ex Odé Collection, HMNS 14992 (5); Louisiana, 120 mi southwest of Marsh Island, D. Moore!, ANSP 209696 (12 valves); Louisiana, 98.5 mi SSE of Cameron, Three Hickey Rock, 28°20'45"N, 92°26'30"W, shale dome, Northwest Gulf Survey Collection Sta. 1679 (lot 20352), diver, 50–60 ft (15–18 m), 07 July 1972, HMNS 7437 (3 valves); Louisiana, mouth of Mississippi River, mudlumps at South Pass, Northwest Gulf Survey Collection Sta. 1684 (lot 19515), surface collected, E. & H. Vokes!, HMNS 7363 (500+ valves); Texas, 74 mi SSE of Galveston, Stetson Bank, dredged, 10–50 fms (18–91 m), Northwest Gulf Survey Collection Sta. G3Sh17 (lot 7380), T. E. Pulley & P. McGee! 1963, HMNS 7345 (1650 valves); Texas, 32.5 mi N of Port Isabel, 26°36'N, 97°08'W, trawl, 12 fms (22 m), Northwest Gulf Survey Collection Sta. G32W61 (lot 5101), GUS III, 10–25 August 1965, HMNS 7347 (9 + 249 valves). BAHAMAS: New Providence Island, Nassau Harbor, dredged, AMNH 80773 (1 + 4 valves); Andros, Fresh Creek, off Coakley Town, 400 fms (732 m), MOTHER GOOSE II, J. Armstrong!, June 1950, AMNH 134068 (1 valve); Bimini Island, 03 September 1947, AMNH 91429 (1 valve).

Vouchers for this study: FK-104 (AMNH 290090, 35 specimens); FK-106 (AMNH 290087, 500; DMNH 209190, 100; FMNH 278463, 100; UMMZ 255298, 10+).

Varicorbula krebsiana (C. B. Adams, 1852) (9 lots, 100 specimens): JAMAICA: DMNH 21941 (1 paralectotype, ex ANSP 297148 [2 paralectotypes, *vidi*]]; C. B. Adams!, ANSP 297148

(2); ex Haines Collection, AMNH 33808 (1); ex Swift Collection, ANSP 50899 (3); Kingston Harbor, between Kingston and Port Royal, 3–4 fms (5.5–7 m), [muddy bottom, *fide* C. B. Adams, 1852: 234], C. B. Adams! [Acc. 1173, ex C. B. Adams Colln., exch. Amherst College, 1942] MCZ 155611 (1 lectotype, with note "spec. fig'd by Dall" [1886: pl. 1, figs. 1, la, b]); same data, MCZ 155612 (paralectotypes: 10 + 26 each separated right and left valves, 2 fragments); same data, ex MCZ ex Adams Collection, ANSP 182624 (paralectotypes, 4 + 1 valve). PUERTO RICO: Montalva Bay, Enunado, J. Poling!, AMNH 85095 (21 + 4 valves), FMNH 278465 (12, ex AMNH 85095); Laurel Reef, off La Parguera, dredge, 75 ft (23 m), G. L. Warmke! 15 June 1956, ANSP 222748 (5 + 6 valves).

Varicorbula philippii (E. A. Smith, 1885) (37 lots, 402+ specimens). BERMUDA: 1.5 mi (2.4 km) south of Castle Roads channel, J. Lightbourn!, 13 September 1975, DMNH 106570 (2); 1.5 mi (2.4 km) south of Castle Roads channel, dredged 40–60 fms (73–110 m), J. Lightbourn!, 13 September 1975, ex R. Jensen Collection, DMNH 202580 (1 valve). NORTH CAROLINA: R/V EASTWARD sta. 10496, 34°09.5' to 34°10'N, 76°09.7'W, 50 m, Day dredge, Porter & Jenner!, 08 October 1968, NCSM/IMS P-4693 (1); R/V DAN MOORE sta. #0365, SSE of Cape Hatteras, 35°00'N, 75°28'W, scallop dredge, 26 fms (47 m), H. J. Porter!, 01 October 1968, NCSM/IMS 3186 (58, incl. 2 live collected). EASTERN FLORIDA: R/V JOHNSON Cr. 005, JOHNSON-SEA-LINK-I dive #274, 27°10.7'N, 80°02.7'W, off St. Lucie Inlet, Martin County, 22.9 m, T. Askew! (lockout diver), 25 July 1975, HBOM 064:01118 (2); R/V GOSNOLD Cr. 222, Sta. 267b, 27°08.2–08.0'N, 080°00.0–079°59.7'W, 62 m, Smith-McIntyre grab, D. K. Young!, 26 February 1974, HBOM 064:00657 (1); off Palm Beach County, 30 fms (5.5 m), Donovan!, July 1940, AMNH 128166 (20); off Palm Beach County, 3 fms (55 m), Donovan!, July 1946, AMNH 129433 (2); off Palm Beach, dredged, T. L. McGinty!, June 1940, ANSP 178586 (4) and DMNH 21944 (1, ex ANSP 178586); off Palm Beach, dredge, 300 fms (549 m), ex Bales Collection no. 12452, ANSP 221298 (4); off Palm Beach Inlet, dredged, 50 fms (91.5 m), July 1940, AMNH 144099 (21 + 3 valves); Lake Worth, Boynton [Beach], T. McGinty! June 1938, ANSP 174911 (1); east of Government Cut, Miami, 27 fms (49 m), rocky, T. L. Moise!, 30 April 1954, ANSP 194291 (6). WESTERN FLORIDA (GULF OF MEXICO): Gulf of Mexico, J. Moore!, FMNH 165115 (4); Pelican Shoal [Lower Florida Keys], J. B. Schwengel!, 1940, FMNH 77960 (16 valves); off Dry Tortugas, 280 ft (85 m), dredge, J. Moore! October 1969, ex Sartor Collection, HMNS 35531 (1); southwest of John's Pass, 27 fms (49 m), Steger! 1965, ANSP 306297 (in part) (4); southwest of John's Pass, D. Steger!, DMNH 21943 (ex ANSP 306297) (1); south-southwest of John's Pass, 34 fms (62 m), D. Steger!, 1977, DMNH 124336 (8) and DMNH 124339 (50+); south-southwest of John's Pass, 29 fms (53 m), D. Steger!, 1977, DMNH 124326 (3) and DMNH 124343 (3); south-southwest of John's Pass, 27 fms (49 m), D. Steger!, 1977, DMNH 124332 (50+); southwest of Anna Maria Island, dredged, 300–400 ft (91–122 m), J. Moore!, AMNH 232603 (4) and HMNS 962 (in part) (1); west of Anna Maria Island, dredged, 400 ft (122 m), J. Moore!, Summer 1964, ex Bijur Collection, AMNH 248383 (21 + 27 valves); off Egmont Key, dredged, J. Moore!, 170 ft (52 m), April 1996, ex Hicks Collection, AMNH 248935 (10 + 10 valves); west of Egmont Key, 300 ft (91 m), J. Moore!, July 1964, ex Germer Collection, AMNH 232604 (2). TEXAS (GULF OF MEXICO): Stetson Bank, 74 mi SSE of

Galveston, dredged, 10–50 fms (18–91 m), Northwest Gulf Survey Collection Sta. G3Sh17 (lot 7380), T. E. Pulley & P. McGee!, 1963, HMNS 7345 (in part) (5 + 9 valves). ANTILLES: Grand Cayman, George Town Harbor, by the stack, A. J. Ostheimer III! sta. D-15, ANSP 209868 (1); Dominican Republic, Pt. Trujillo, outside Yuncu Reef, 15–25 fms (27.5–46 m), D. Pease!, 1933, AMNH 94671 (7 + 13 valves); same as previous, D. Pease!, 1932, AMNH 94733 (7 + 11 valves); Virgin Islands, St. John, ex Stamford Museum, DMNH 185976 (1); Grenada, West Grenada, Grand Mal Bay, "Fontenoy," 36–48 ft (11–15 m), shell/sand/grass, R. Ostheimer! 12 February 1964, ANSP 297010 (1); Tobago, Scarborough, 2 mi south of Fort George, 36 fms (66 m), R. W. Foster! 20 April 1950, ANSP 246146 (2 valves). CENTRAL AMERICA: British Honduras [Belize], west of Blue Ground Range, Main Channel, 16°48'10"N, 88°09'20"W, sta. 72, soft mud, 79 ft (24 m), R. Robertson!, 15 August 1961, ANSP 283001 (3).

For comparative purposes:

Varicorbula gibba (Olivi, 1792): Heligoland Island, Germany, W. Mansen!, AMNH 92367 (20+ valves); Lubworth Bank, Dorset, English Channel, A. Brokershire!, Lanning Coll., AMNH 275995 (6) and AMNH 275996 (5); Dublin Bay, Ireland, Germer Coll., AMNH 260456 (10 valves); La Val André, Bretagne, France, April 1966, AMNH 178089 (2); Patras, Greece, Nelson Coll., FMNH 158519 (6 + 1 valve).

Notocorbula vicaria Iredale, 1930: Australia, Haines Coll., AMNH 33845 (6).

RESULTS

Varicorbula Grant & Gale, 1931

Varicorbula Grant & Gale, 1931:12, footnote to p. 420.—Vokes, 1945:12, 13.—Keen, 1969:N695.—Anderson, 1996:20.

For list of previously accepted synonyms, see Vokes, 1945: 12.

Type species: *Tellina gibba* Olivi, 1792, by original designation; western Europe and the Mediterranean Sea (and introduced to Australia; Lamprell et al., 1998).

Diagnosis: Shell trigonal, rather thin but sturdy, bluntly truncated posteriorly, strongly inequivalue; left valve smaller, flatter, less rostrate; right valve larger, more inflated. Both valves concentrically sculptured, but discrepantly so; right valve with coarser, higher ridges; left valve with finer concentric ridges, crossed by radial ridges. Umbones prosogyrous, higher and more inflated in right valve, without nepionic caps. Periostracum on the left valve forming overlapping foliations and radial lines, overhanging shell edge substantially. Right valve with large knob-shaped tooth, articulating with deep socket in left valve. Elongated plate ("left cardinal tooth" of Yonge, 1946:fig. 2) posterior to socket of left valve, including resilium-bearing chondrophore; complimentary right chondrophore on shelf within embayment posterior to tooth. Resilium oriented dorsoventrally; external ligament very small. Lateral teeth absent. Interior shell margins smooth. Deep interior groove running parallel to ventral edge of right valve, and continuing into lateral lamellae

on either side of hinge, into which margin of left valve inserts. Anterior muscle scar moderately large and crescent-shaped; posterior muscle scar oval and slightly larger. Pallial line entire (but interrupted by small gaps); pallial sinus shallow but distinct.

Remarks: No recent morphology-based phylogenetic hypothesis has yet been attempted for this family, nor are there sufficient data (conchological and/or non-conchological) to attempt one at this point. The last taxonomic revision of Corbulidae, based entirely on shell characters, was by Vokes (1945), who recognized 21 genus-group names as valid. *Varicorbula* Grant & Gale, 1931, is the appropriate genus for the present material following the diagnoses of Vokes (1945), Keen (1969), and Anderson (1996). The present material also agrees in currently accepted genus-level characters with Recent European specimens identified as *V. gibba* in the AMNH and FMNH collections and with the descriptions of the latter species by Bucquoy et al. (1896) and Yonge (1946). Although some subsequent authors (Vaught, 1989; Anderson, 1996) have adopted use of a large genus *Corbula* containing numerous conchologically defined subgenera, we treat *Varicorbula* as a full genus, in the absence of compelling reasons to support subtaxonomic categories, following Vokes (1945) and Lamprell et al. (1998).

Varicorbula is one of three recognized corbulid genera with strongly inequivalue shells (the other two being *Corbula* and *Notocorbula*); all are posteriorly rostrate and concentrically sculptured. According to Vokes (1945), *Varicorbula* is distinguished from the other two by discrepant sculpture on right and left valves, a non-rostrate smaller left valve, lacking lateral hinge teeth and a nepionic cap (= nepioconch; "resting stages" of Stenzel et al., 1957; "juvenile shell" of Iredale, 1930; characteristic of *Notocorbula*, *fide* Vokes, 1945) on the valves (which in other genera indicates subequal valves in the juvenile), and in being strongly inequivaled even as juveniles. Species of *Varicorbula* also have radial ridges (enhanced by periostracum called "epidermis" in the older literature; ridges also detectable on fossil shells) on the smaller left valve [e.g., *gibba*: Sowerby, 1820–1824:pl. 49, no. 1; Reeve, 1843:pl. 2, figs. 10a, b; Vokes, 1945:pl. 1, fig. 15; Tebble, 1966:fig. 91b; Keen, 1969:pl. E156, fig. 8d; Nordsieck, 1969:149, pl. 21, fig. 84.00; Rolán Mosquera et al., 1990:fig. 172; AMNH 275995, *vidi*; *caloosae* Dall, 1898:853 [text only]; Olsson & Harbison, 1953:pl. 13, fig. 10a; *chipolana* Gardner, 1928:pl. 34, fig. 17; *chowanensis* Bailey, 1977:fig. 1b; *islatrinitatis* Maury, 1925: 253, pl. 19, fig. 10 (also Jung, 1969:pl. 40, figs. 1, 2; Woodring, 1982:pl. 120, fig. 1); *limatula*: Vokes & Vokes, 1984:pl. 47, fig. 7c; *philippii*: Vokes & Vokes, 1984:pl. 47, figs. 7a; Figure 27; *puntacordensis* Weisbord, 1964: pl. 57, fig. 15; *sanctidominici* Maury, 1925 (Anderson, 1996:pl. 3, fig. 16); *waltonensis* Gardner, 1928:pl. 34, fig. 21]. Abbott (1974) and Lamprell et al. (1998) considered

this last feature characteristic of the genus *Varicorbula*, although radial ridges are also known in some members of Caestocorbulinae (see Discussion).

Although not noted by Lamprell et al. (1998), radial ridges are also present on the left valve in species of *Notocorbula* Iredale, 1930 [*N. vicaria* (type species; + *tunicata* Hinds, 1843) Iredale, 1930:pl. 65, fig. 4; Keen, 1969:pl. E156, fig. 1b; AMNH 33845; *N. hydropica* Iredale, 1930:pl. 65, fig. 6; *N. texana* (Gabb, 1860); Stenzel et al., 1957: pl. 21, figs. 3, 5]. *Notocorbula* has been previously considered the senior synonym of *Varicorbula* (teste Stenzel et al., 1957; followed by Warmke & Abbott, 1961; Weisbord, 1964; Jung, 1969), based on the presence of "subdued" nepionic caps in the type species of *Varicorbula*, *V. gibba*. This explains the use of *Notocorbula* for *V. disparilis/limatula/operculata* by some authors (Warmke & Abbott, 1961; Odé, 1965, 1971; Bock & Moore, 1968; Odé & Spears, 1970; McGinty & Nelson, 1972; Morris, 1973; Porter, 1974, 1975; Rios, 1970). *Varicorbula gibba* indeed sometimes has irregular growth stoppages that could be interpreted as nepionic caps, but the presence of these is inconsistent, they are sometimes evident only on the larger right valve, and they are identically sculptured with the remainder of the valve (AMNH 92367, 275995, 260456). They are almost completely absent in the present Florida Keys material. In *Notocorbula*, the cap is invariably present in both valves and is more weakly (if not differently) sculptured from the rest of the valve (Iredale, 1930:404, 405; Vokes, 1945:pl. 1, figs. 6–10; Stenzel et al., 1957:pl. 21, figs. 2, 3, 5, 8; Keen, 1969:pl. E156, figs. 1a–c; AMNH 33845). There are many conchological similarities between *Notocorbula* and *Varicorbula*: similar hinge structure, nearly identical pallial lines and sinuses, and a smaller left valve with weaker concentric sculpture, radial sculpture, and heavier periostracum than in the right valve. The nepionic cap, when present, varies in size within a species in both genera. The keeled cardinal tooth in the right valve of *Notocorbula* (considered diagnostic by Iredale, 1930, and Vokes, 1945) does not demonstrably differ from that in *Varicorbula*, and members of both genera have a "peculiarly bipartite chondrophore" (Vokes, 1945:14, for *Notocorbula*; also Keen, 1969) also apparently present in other genera (e.g., *Caryocorbula*, fide Vokes, 1945; *Vokesula* Stenzel & Twining, in Stenzel et al., 1957). Nevertheless, *Varicorbula* species are overall smaller, less equivalve, thinner shelled, and less rostrate than *Notocorbula* species. Odé (1976) listed *Notocorbula* among those taxa close to *Varicorbula* but needing clarification. We advocate continued use of *Varicorbula* and *Notocorbula* as separate genera until a more comprehensive study of the family, including examination of living animals, can be made (in agreement with Woodring, 1982; Anderson, 1996; Lamprell et al., 1998).

Flexicorbula Chavan, 1947 (based on *Varicorbula* (*Flexicorbula*) *vokesi* Chavan, 1947 [specimens not seen],

a Cretaceous fossil from Palestine, type by original designation) is probably synonymous with *Varicorbula*, the former being similarly inequivale and bluntly rostrate. *Flexicorbula* was originally distinguished from *Varicorbula* by having prosogyrous beaks as well as a distinct lamella posterior to the hinge (a pseudo-lateral tooth, often termed P1) (Chavan, 1947). Observations on museum specimens of *V. gibba* and on the species discussed herein show that *Varicorbula* species are also prosogyrous and also possess a strong P1 (Figures 15, 16).

Vokesula Stenzel & Twining in Stenzel et al., 1957 (based on *Corbula smithvillensis* Harris, 1895, from Eocene to Oligocene of North America, type by original designation) also appears very similar (Stenzel et al., 1957:pl. 21, figs. 11–29, pl. 22, figs. 1–6; Keen, 1969:pl. E156, figs. 7a–c), except that the smaller left valve is nearly smooth (i.e., without radials?) and nepionic caps are clearly evident on both valves (although the original authors [Stenzel & Twining in Stenzel et al., 1957:173, 176] described a "neanic portion" yet claimed the umbones to be "generally not set off by a resting stage"). Odé (1976:28) also recognized the similarity, and likewise left it unresolved, noting only that the status of *Vokesula* relative to *Varicorbula* "needs to be clarified."

Caryocorbula Gardner, 1926 (based on *Corbula alabamensis* Lea, 1833, from the western Atlantic Eocene, type by original designation), has been used by some authors without explanation for some of the species here under consideration (Johnson, 1934; McLean, 1936; Aguayo & Jaume, 1950; Abbott, 1974). *Caryocorbula* is characterized as only slightly inequivale and similarly sculptured on the right and left valves (Gardner, 1926; Vokes, 1945; Stenzel et al., 1957). Its application to the species is perhaps due to mention of "a microscopically fine radial lineation" (Gardner, 1926: 46), which is however distinctly different from the radial ridges present in *Varicorbula*.

Varicorbula disparilis (d'Orbigny, 1842)

(Figures 1–25)

Selected synonymy:

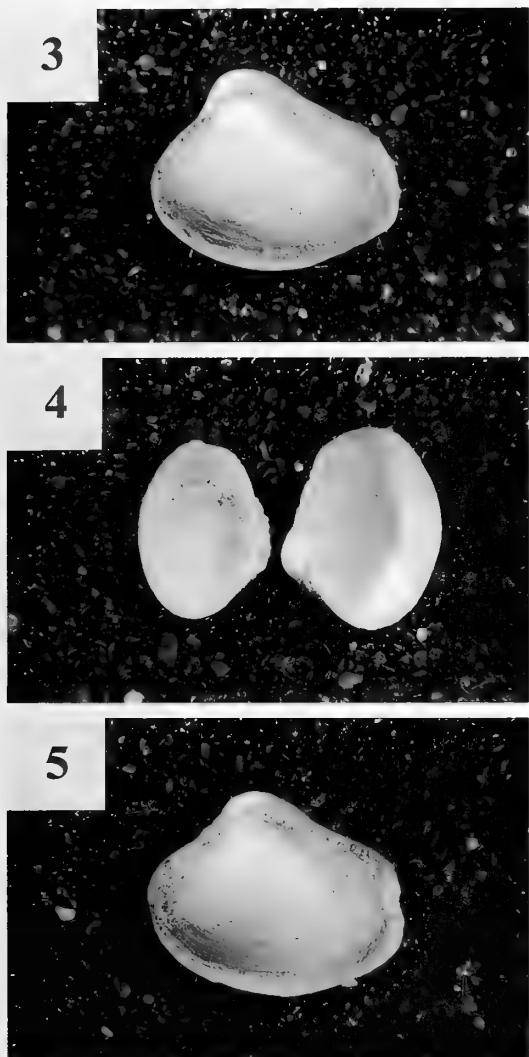
Corbula disparilis d'Orbigny, 1842:pl. 27, figs. 1–4; 1853: 283 (sp. no. 484). Type locality: Guadeloupe.

Corbula disparilis d'Orbigny, 1846 [sic].—Dall, 1886:314–315, pl. 1, figs. 4, 4a, b; 1889:70, 71, pl. 1, figs. 4, 4a, b [after Dall, 1886].—McLean, 1951: 114, pl. 23, fig. 11 [after Dall, 1886].

Corbula disparilis d'Orbigny, 1853 [sic].—Dall, 1881:115. —Baker, 1965:105.

Corbula disparilis d'Orbigny.—M. Smith, 1937:67, pl. 60, figs. 4a, b [after Dall, 1886]; 1940:120, sp. 1557, figs. a, b [after Dall, 1886]; 1941:67, pl. 60, figs. 4a, b [after Dall, 1886]; 1945:67, pl. 60, figs. 4a, b [after Dall, 1886]; 1951:67, pl. 60, figs. 4a, b [after Dall, 1886].

Corbula limatula Conrad, 1846 (Feb.): 25, pl. 1, fig. 2. Type locality: Gulf of Mexico, off the coast of Florida.—

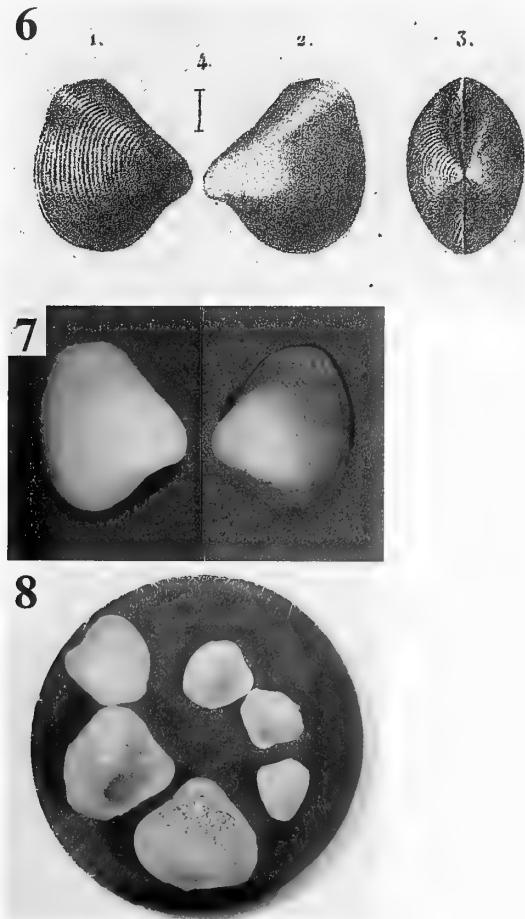


Figures 3–5. *Corbula limatula*, ANSP 50909, type material. Figure 3. Articulated paralectotype, 8.0 mm length. Figure 4. Disarticulated paralectotype, larger valve = 6.6 mm length. Figure 5. Articulated lectotype (ANSP 50909a), 8.3 mm.

Lamy, 1941:228 (remark only, within section *Cuneocorbula*).—Baker, 1964:67 (lectotype designation); 1965:104–105.

Varicorbula operculata (Philippi, 1848).—Abbott, 1974: 538, text-fig. 5996 [after Dall, 1886].—Vokes & Vokes, 1984:45, pl. 47, fig. 7c only.—Lyons, 1989:61, pl. 18, figs. 1a, b.—Abbott & Morris, 1995:103, text fig. 33 [after Dall, 1886], pl. 23, fig. 11 bottom specimen only (color).

Diagnosis: *Varicorbula* of 5–9 mm shell length, whitish with persistent rose-colored margins dorsally. Radial ridges on left valve weak, restricted to anteroposterior slopes and near shell margins. Truncation:height ratio (= height of truncated posterior edge of right valve versus total dorsoventral height) 42–46%.



Figures 6–8. *Corbula disparilis*. Figure 6. Original illustrations from d'Orbigny in Sagra, 1842. Scale bar (d'Orbigny's fig. 4) = 5.4 mm. Figures 7, 8. Syntypic lot (BMNH 1854.10.4.550). Figure 7. Two largest valves: right valve (at left, lectotype here designated), 5.1 mm length; left valve (at right, not conspecific), 5.0 mm length. Figure 8. Other six valves; smallest (left) valve, 2.3 mm length.

Taxonomy: Although the species of the present material has been most often called *Varicorbula operculata* (Philippi, 1848) in the literature, an earlier name exists. *Corbula disparilis* d'Orbigny, 1842, described from Guadeloupe, has most often appeared as the senior synonym of the species names discussed here, based on the assumed date of publication (see below) (e.g., Bush, 1885a; Dall, 1886; Guppy & Dall, 1896; Dall & Simpson, 1901; Mauvy, 1920; Lamy, 1941; McLean, 1951; M. Smith, 1937, 1941, 1945, 1951; Anderson, 1996, with “?”; Lee, 2000). Some other authors (Pulley, 1953; Abbott, 1954, 1974; Rios, 1975, 1985, 1994; Jensen & Harasewych, 1986) have used *V. operculata* as the senior synonym, considering *C. disparilis* “of authors, non d'Orbigny,” as synonymous. Still other authors (Warmke & Abbott, 1961; Morris, 1973; Abbott & Morris, 1995) have listed *C. dis-*

parilis d'Orbigny in synonymy or as a previous name without further comment.

Baker (1965) noted that the original figures of *Corbula disparilis* show a decidedly subequivalve shell (d'Orbigny, 1842:pl. 27, figs. 1–3; reproduced in Figure 6), and concluded that it is most likely not conspecific with *Varicorbula operculata*. Dall (1886), however, considered d'Orbigny's figures inaccurate or based on separated valves without periostracum, because the original text description (d'Orbigny, 1853:283) indicated that the shells are inequivalve (also reflected by the etymology of the name). Examination of the syntypic lot of *C. disparilis* (BMNH 1854.10.4.550, *vidi*; Figures 7, 8) revealed that Dall was indeed correct and that Baker was not. This lot contains eight disarticulated valves (six right valves, two left valves), none of which are paired. The six small valves (five right; one left; 4.6–2.3 mm; Figure 8) assuredly belong to a species of *Varicorbula*. The five small right valves are somewhat thin-shelled, heavily sculptured, and have interior peripheral grooves for the edge of the smaller left valve; their truncation:height ratios vary widely (39–52%) across the range noted in *V. disparilis*, *V. krebsiana*, and *V. philippii* (see below), and are thus inconclusive. The small left valve (2.3 mm) lacks defining periostracum and radial ridges; it is thin-shelled and weakly sculptured but is otherwise uninformative.

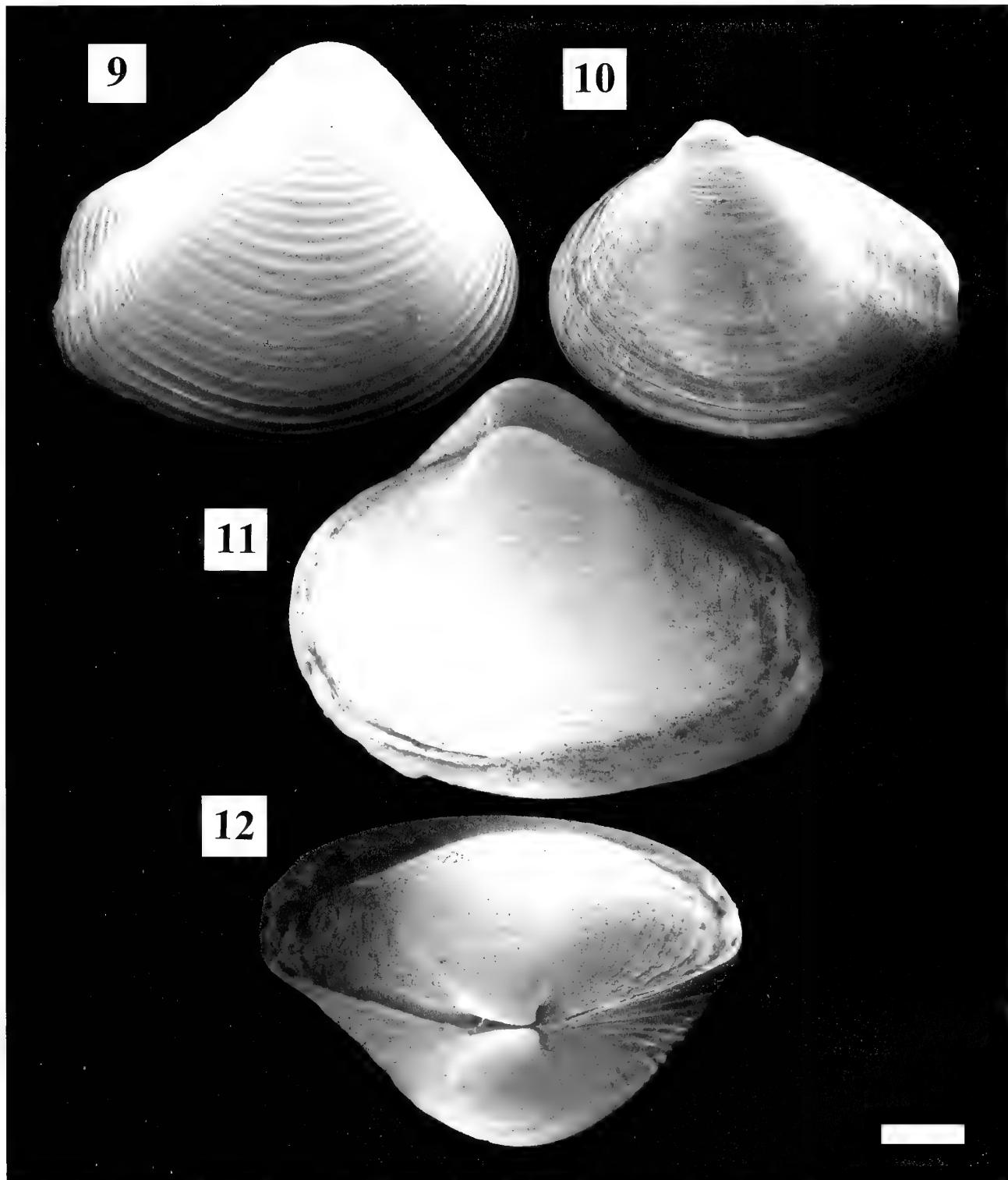
The two largest valves of the syntypic lot of *Corbula disparilis* (right valve 5.1 mm, left valve 5.0 mm length; Figure 7), however, appear to form a single nearly equivalve pair when viewed side-by-side; this is presumably what d'Orbigny's illustrator assumed. The large left valve (Figure 7, at right; probably also illustrated by d'Orbigny, 1842:pl. 27, fig. 2, reproduced in Figure 6) is thick-walled and stained black (the other seven valves are all whitish); it is not likely conspecific with the rest, nor (on the basis of sculpture) congeneric. The large right valve definitely belongs to a species of *Varicorbula*. It appears to be the right valve illustrated by d'Orbigny (1842:pl. 27, fig. 1; reproduced in Figure 6), and although it does not exactly match the published figure (which has a truncation:height ratio of 34%, too small for *C. disparilis*; see below), the latter probably suffers from the "artistic license" noted in other d'Orbigny figures (Mikkelsen & Mikkelsen, 1984: figs. 6C, D). Because this large right valve (Figure 7, at left) is also closest in size to the illustrated length bar (5.4 mm; d'Orbigny, 1842:pl. 27, fig. 4), we here designate this valve (5.1 mm; truncation:height ratio 45%) as the lectotype of *C. disparilis*. The six small valves are considered paralectotypes, but are acknowledged as being of problematic identification. The large left valve is here excluded from the syntypic series.

The original material of *Corbula limatula* Conrad, 1846, was interestingly similar to the present collections, being "dredged up on the sounding lead in deep water off the coast of Florida." The syntypic lot (ANSP 50909, *vidi*) contains three valve pairs (Figures 3–5), virtually

identical in morphology to those of the present collections (Figures 9–12) and to the lectotype of *Varicorbula disparilis*. Baker (1964) gave the "type" of *C. limatula* as ANSP 50909a, of 8.2 × 6.3 mm, an act that constitutes a lectotype designation. Although the three specimens of the ANSP lot have since been reunited, it is reasonable to assume the specimen closest to these stated dimensions (largest syntype, 8.3 × 6.6 mm; Figure 5) is the lectotype, and this has now been resegregated as such. The remaining two syntypes can now be considered as paralectotypes. This species' yellow-and-pink shell coloration has a tendency to turn to white-and-brown in older collections, as mentioned in Conrad's (1846) description and as seen in other museum material (e.g., AMNH).

This discussion stops short of synonymizing *Corbula operculata* Philippi, 1848, with *Varicorbula disparilis*, although most previous authors have considered them conspecific, and it seems likely that this is true. Baker (1965) noted the closeness of *V. disparilis* [as *C. limatula*] with *C. operculata*, the latter described from St. Thomas, on mud at 15–18 fathoms. Philippi's (1848:13) description reads [our translation from the original Latin]: "shell heart-shaped triangular, very inequivalve, anteriorly subtruncated, white, right [sic] valve small, smooth, brownish, the left [sic] deeply transversely sulcated, the apex inrolled, the regions of the lunula and area brown." A search for the type material of this species was unsuccessful (not in Humboldt Museum, Berlin, M. Glaubrecht, in litt., July 1997; not in BMNH, J. D. Taylor and K. Way, in litt., February 1998; ?in Museo Nacional de Historia Natural, Santiago, Chile, no reply; ?in Übersee-Museum, Bremen, Germany, no reply). Because the unillustrated original description is inadequate to distinguish *V. operculata* from other western Atlantic species, and the only material from the Virgin Islands that we have seen is in fact *V. philippii*, synonymy cannot confidently be made without examination of type material. Until Philippi's original specimens can be located, *Corbula operculata* must be considered a *nomen dubium*.

The original publication dates of d'Orbigny's numerous western Atlantic bivalve descriptions in Sagra's *Histoire physique, politique et naturelle de l'Ile de Cuba* are of considerable uncertainty. Although this controversy is not the prime subject of this report, its outcome determines the date of publication for *Corbula disparilis*, and thus the priority status of this name relative to *C. limatula* and *C. operculata*. For this reason, we here provide a brief summary of the evidence that has led us to consider *C. disparilis* as the oldest name. d'Orbigny's "Sagra Report" was originally published in French, and later translated into Spanish [as *Historia fisica politica y natural de la Isla de Cuba*]. The former was issued in two volumes of text and one of plates, each apparently published in small installments (livraisons), the individual dates of which have never been definitively compiled. Volume 1 of the French edition dates from 1840/41–1842 and vol-



Figures 9–12. *Varicorbula disparilis*, FK-106, scanning electron micrographs. Figure 9. Larger (right) valve. Figure 10. Smaller (left) valve. Figures 11, 12. Articulated specimens. Scale bar = 1 mm (for 9–12).

ume 2 from 1842–1853 (Aguayo, 1943; G. Rosenberg, personal communication).

Three dates have been given for *Corbula disparilis* d'Orbigny in the literature: 1842, 1846, and 1853. The text description for *C. disparilis* (vol. 2, p. 283) was almost certainly published in 1853, but if (as certain authors claim) the Atlas pages on which this species was named and figured (pl. 27, figs. 1–4; making the name taxonomically available) were published earlier, the date would derive from that of the Atlas. A number of authors (Dall, 1885; Aguayo, 1943 [citing earlier authors]; Petit & Harasewych, 1990) have claimed that the French atlas appeared in 1842 (as a unit rather than livraisons), concurrent with the completion of volume 1, and indeed this is the date most frequently applied to the various bivalves of d'Orbigny (e.g., Abbott, 1974; Turgeon et al., 1998). 1853 is the latest date by which all of d'Orbigny's French work, text or plate pages, would have been published. This is the date applied to *C. disparilis* by Dall (1881), Baker (1965), and G. Rosenberg (personal communication), and as previously mentioned is probably the date of the text description. Some of the *Corbula* species in this volume are referenced as "d'Orb. 1846" (referring to the Spanish edition? see below) while others (including *C. disparilis*) are given merely as "d'Orb.>"; this implies that the text indeed appeared later than 1846. As evidence in support of 1853 for *C. disparilis*, Baker (1965) noted that none of d'Orbigny's *Corbula* species were covered by C.B. Adams (1852); the earliest citation of d'Orbigny's bivalves located by G. Rosenberg (personal communication) is Mörcz (1852), which lacks d'Orbigny's *Corbula* species as well. The date 1846 as used by some authors apparently derives from the appearance of *C. disparilis* in the Spanish edition, published as a single volume. Because the French text for *C. disparilis* likely dates from 1853, either the year 1846 is incorrect or (more likely) the Spanish translation predates the original French (?produced from the unpublished French manuscript). Based on the above uncertainties, we conservatively consider the publication date of *C. disparilis* as 1842, but note, in the event that subsequent research determines a later date, that *C. limatula* Conrad, 1846, could gain seniority as the earlier name.

The geologic range of *Varicorbula disparilis* extends back into the Middle Cenozoic. Maury (1920) considered it as Pliocene to Recent, but presented data only for the Pleistocene. Other Tertiary reports are the Mio/Pliocene of Panama and Costa Rica (Woodring, 1982), the Mio/Pliocene of Trinidad (Jung, 1969; as *Notocorbula* cf. *disparilis*), the Tertiary of the Dominican Republic (Gabb, 1873) and the Oligocene of Jamaica (Guppy & Dall, 1896).

Several additional names have been introduced for members of this group in the Cenozoic western Atlantic: *Corbula vieta* Guppy, 1866 (Trinidad, Jamaica); *Erycina tensa* Guppy, 1866 (Trinidad); *C. isla-trinitatis* Maury,

1925 (Trinidad, Panama, Venezuela); *C. (Varicorbula) heterogena* Guppy in Dall, 1898 (Jamaica); *C. (V.) sanctidominici* Maury, 1925 (Dominican Republic); *V. sanctianderaea* Maury, 1925 (Trinidad); *V. baea* Woodring, 1982 (Panama); *V. waltonensis* Gardner, 1928 (Florida); *C. (Aloidis) calosae* Dall, 1898 (Florida); *V. chipolana* Dall in Gardner, 1928 (Florida); *C. (Notocorbula) bruscasensis* Weisbord, 1964 (Venezuela); *C. (N.) puntagordensis* Weisbord, 1964 (Venezuela); *V. chowanensis* Bailey, 1977 (North Carolina). Although many of these have been compared with *V. disparilis* or its synonyms and congeners discussed herein (Gabb, 1873; Guppy & Dall, 1896; Dall, 1898; Maury, 1917; Olsson & Harbison, 1953; Anderson, 1996), they have not been critically re-examined here. Even if any of these are ultimately found conspecific with *V. disparilis*, this would not change the earliest name of the extant taxon.

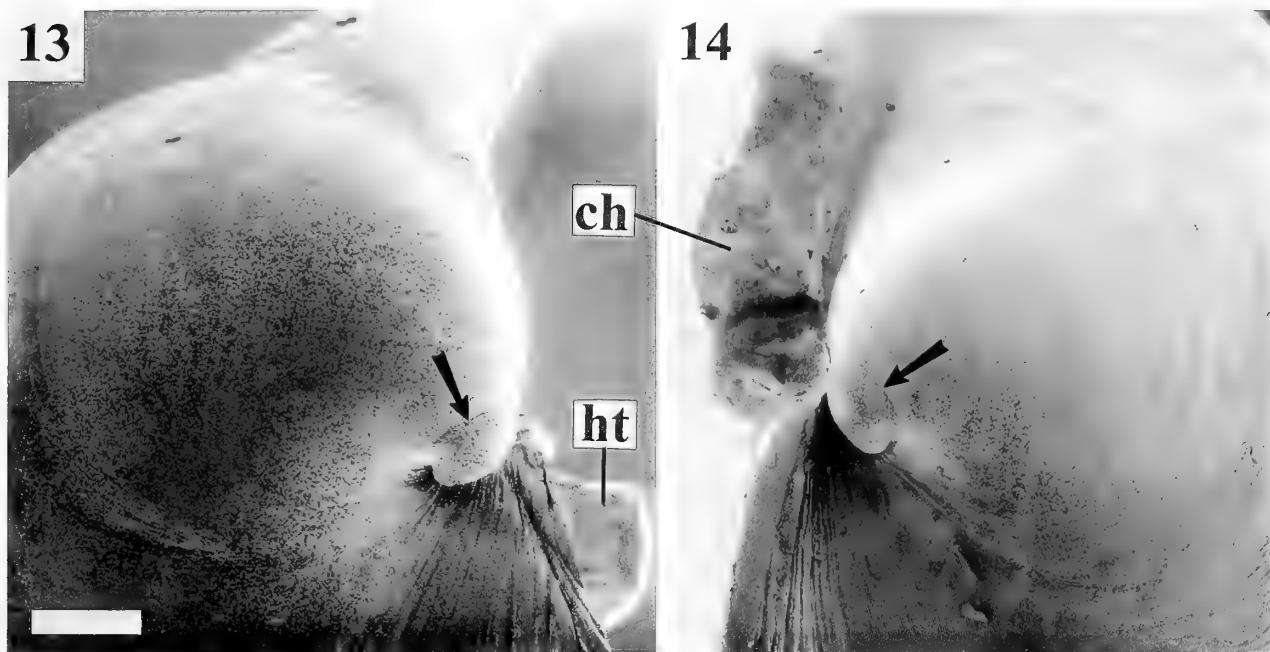
Shell: The shell of *Varicorbula disparilis* (Figures 9–12) ranges from 5–9 mm in length (larger valve measured; min. = 4.6, max. = 8.7, mean = 6.6 ± 0.8 SD [standard deviation], n = 100). In life the shell is whitish with a light yellow blush (especially at the umbones), and dorsal rose-colored margins to either side of the umbones, and usually also on the posterior slope of the smaller left valve; empty shells are white with persistent rose margins.

The prodissoconch (Figures 13, 14) is composed of a small embryonic shell (prodissoconch I) of ca. 200 μm diameter, separated from the larger larval shell (prodissoconch II) by a distinct growth line, indicative of planktic development. The larval shell is ca. 1.5 mm in anteroposterior length and is separated indistinctly from the dissoconch, only by a change in sculpture from smooth to concentrically sculptured.

The inner surface of the valves (Figure 15) has anterior and posterior adductor muscle scars joined by an evenly curved pallial line. Posteriorly the pallial line is sharply angled, forming a shallow embayment (pallial sinus) for the siphons. The posterior scar is broadly oval; the anterior is elongated crescent-shaped; smaller pedal retractor muscle scars abut each adductor scar dorsally near the hinge line. The hinge teeth (Figures 13, 14, 16) and chondrophore (Figure 14) are as described for the genus *Varicorbula* (above).

When closed, the two valves form a tight seal, without gaping, facilitated by the overlapping periostracum of the smaller valve and the peripheral groove for the edge of the smaller valve on the interior surface of the larger valve. Some specimens show calcification of the marginal periostracum on the left valve in the region of the siphons.

Anatomy: Only minor differences were noted here in the soft-body anatomy of *Varicorbula disparilis* (Figures 17–21) versus those reported for *V. gibba* by Yonge (1946) and *Corbula crassa* Hinds, 1843, by Morton (1990).



Figures 13, 14. *Varicorbula disparilis*, FK-106. Prodissococonch, showing distinct growth line (arrows) between prodissococonch I and II. Figure 13. Right (larger) valve, also showing hinge tooth (ht). Figure 14. Left (smaller) valve, also showing chondrophore (ch). Scale bars = 200 μm (for 13 and 14).

The posterior mantle is heavily pigmented with opaque white in a thick "collar" surrounding the short incurrent and excurrent siphons; a brownish interrupted line (persistent after preservation) outlines the combined siphonal openings at the rim. Both siphons are papillate at the margin (Figure 18); the dorsal (excurrent) siphon is edged by a thin flap of tissue presumably forming an apical cone in life (as shown for *Varicorbula gibba* by Yonge, 1946: fig. 5). The remaining mantle edges are fused except for the pedal opening (from just ventral to the anterior adductor muscle to mid ventrally, just behind the heel of the foot), which is also papillate.

The adductor muscles are subequal, with the posterior more rounded and slightly larger. Each is distinctly formed of two parts (presumably "slow" and "quick" components, *fide* Yonge, 1946, and Morton, 1990). Small pedal retractor muscles lie dorsomedial and adjacent to each adductor. There is no pedal protractor muscle anteriorly.

The ctenidia (Figures 20, 21) are nonplicate, homorhabdic, and consist of smaller outer and larger inner demibranchs. Both demibranchs have sparse interlamellar junctions. The labial palps are long and narrow, comprising an inner pair on the anterior surface of the visceral mass, and an outer pair attached to the mantle near the anterior adductor muscle. The inner ctenidial demibranchs terminate anteriorly between the pairs of palps (Category III ctenidium-palp junction of Stasek, 1963) in the vicinity of the mouth. The demibranchs attach pos-

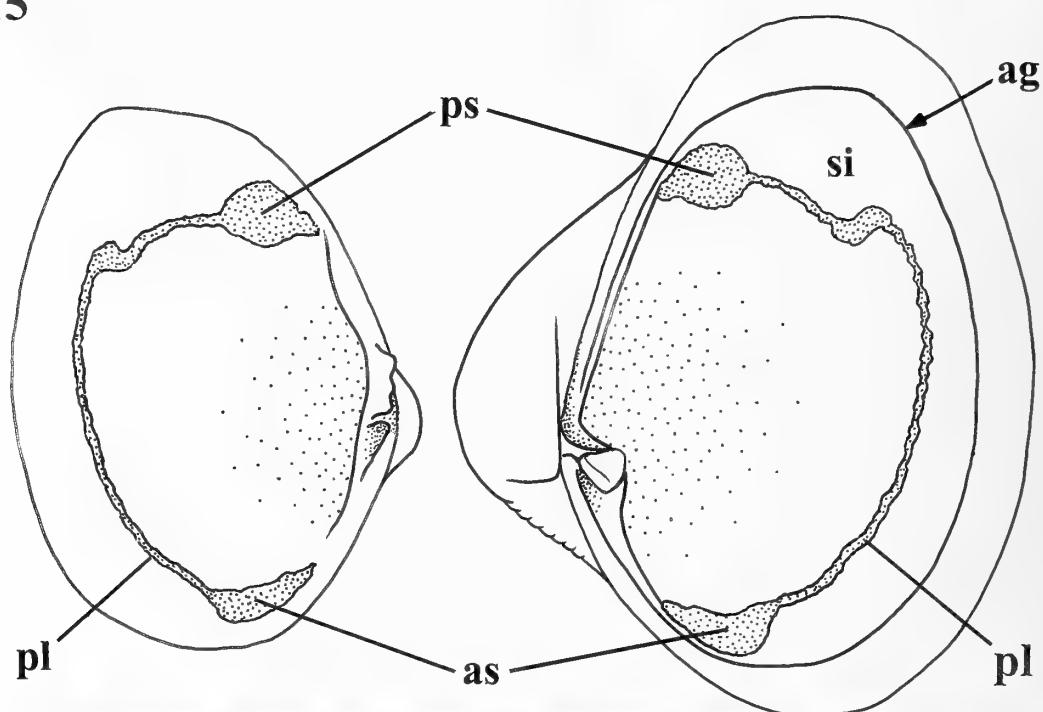
teriorly to the inner membrane between the incurrent and excurrent siphons.

The foot (Figure 19) is narrow, finger-shaped to compressed, translucent white, with an opaque white spherical byssal gland visible through the integument at the "heel." A ventral pedal groove, lined by mucus glands, extends from near the tip to the heel (where the byssal thread emerges). Only single byssal threads are produced.

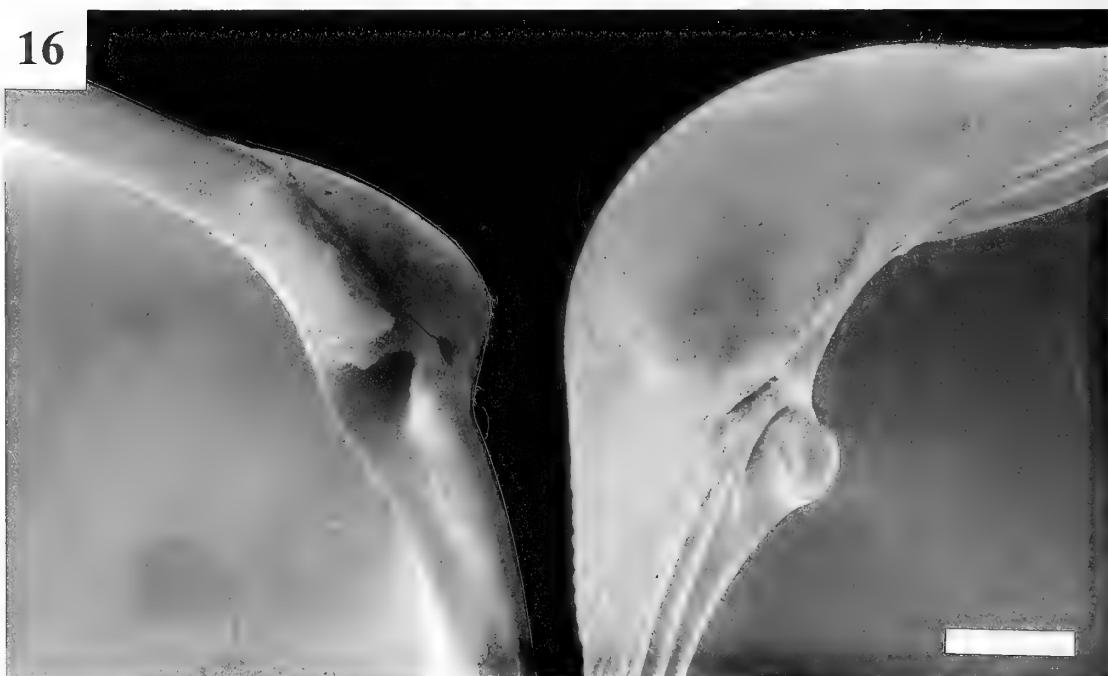
The stomach (Type 5 of Purchon, 1987) occupies the visceral mass, surrounded by whitish gonad and darker digestive gland tissue. The esophagus opens dorsally into the anterior chamber; there is a wide opening to the digestive gland ventrally (actually three adjacent but separate openings according to Purchon, 1960: fig. 17). The posterior part of the stomach includes a large style sac, equipped at the dorsal end with a brownish gastric shield. The midgut conjoins the style sac and parallels its length, emerging from the ventral end of the sac as the intestine. The intestine undergoes a single loop within the gonad (Figure 17; apparently differing from that in *Corbula crassa*, described as having a "series of loops," Morton, 1990: 1067, fig. 14), its typhlosole persisting only until the anteriormost curve of the loop, where it then passes dorsally behind the stomach. The intestine exits the visceral mass posterodorsally, passes through the heart and kidney, over the posterior adductor muscle, and terminates at the anus just dorsal to the excurrent siphon.

Ganglia of the nervous system include small paired cerebral ganglia in the vicinity of the labial palps, a single

15



16



Figures 15, 16. *Varicorbula disparilis*, FK-106. Figure 15. Inner surface of valves (diagrammatic) showing hinge, muscle scars, pallial line, pallial sinus, and groove in the larger (right) valve for articulation of the smaller (left) valve. key: ag, articulation groove; as, anterior adductor muscle scar; pl, pallial line; ps, posterior adductor muscle scar; si, pallial sinus. Figure 16. Hinge, scanning electron micrographs of smaller (left) valve and larger (right) valve. Scale bar = 500 µm (for both views in 16).

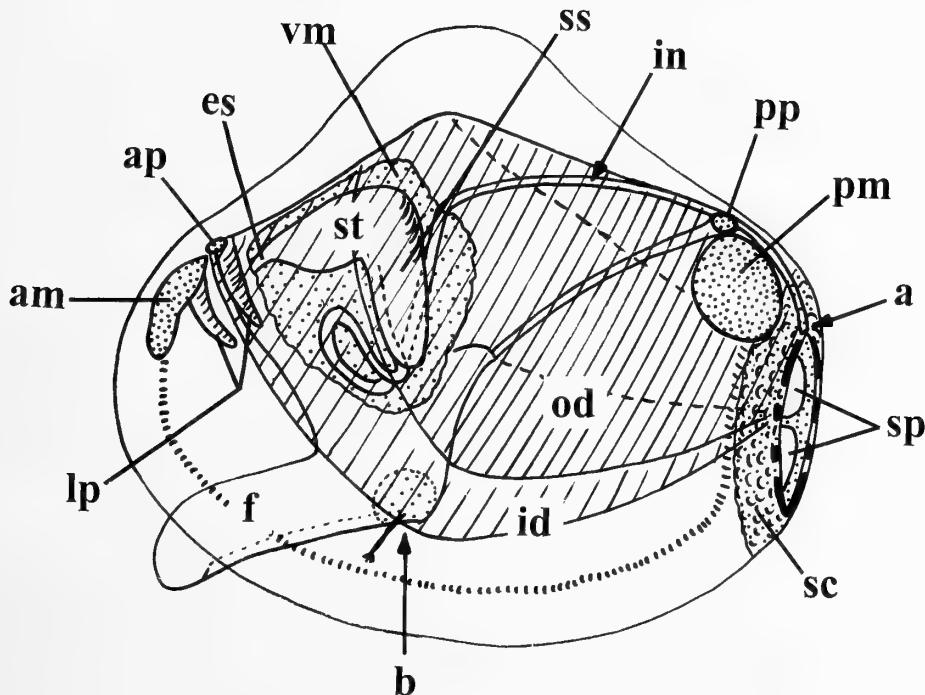


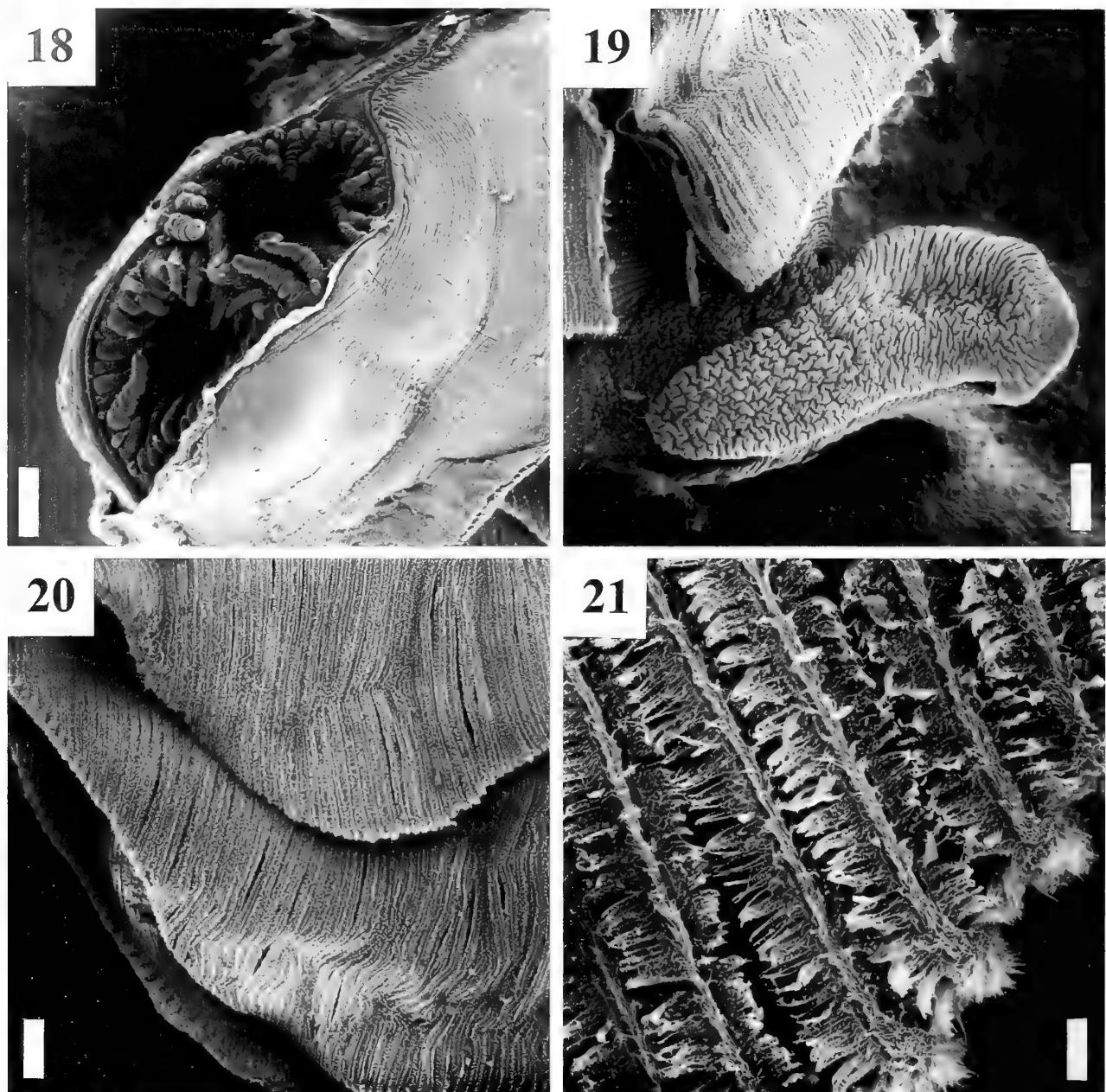
Figure 17. *Varicorbula disparilis*, diagrammatic gross anatomy. a, anus; am, anterior adductor muscle; ap, anterior pedal retractor muscle; b, byssal gland + byssus; es, esophagus; f, foot; id, inner demibranch of ctenidium; in, intestine; lp, labial palp; od, outer demibranch of ctenidium; pm, posterior adductor muscle; pp, posterior pedal retractor muscle; sc, siphonal collar; sp, siphons; ss, style sack; st, stomach; vm, visceral mass (gonad + digestive diverticula).

pedal ganglion in the muscle of the foot, just ventral to the gonad containing the intestinal loop, and a single visceral ganglion in the connective tissue anteroventral to the posterior adductor muscle.

Sexes are separate. Of the two specimens histologically sectioned, one contained only ova in the gonad, while the other contained only sperm. In addition to the presence of interlamellar junctions, there was no additional evidence of brooding (in the form of embryos in the gills).

Distribution: The published geographical distribution of *Varicorbula disparilis* (as *V. operculata* or *V. limatula*) most commonly includes at least the southeastern United States, the Gulf of Mexico, and the West Indies (e.g., Dall, 1889; Johnson, 1934; Warmke & Abbott, 1961; Abbott, 1974; Merrill et al., 1978). However, our observations of museum collections indicate that up to three species have been combined under the single species name. Therefore, all published references and localities require verification either through published figures or, preferably, museum specimens. Verified localities for *V. disparilis* (through specimens or recognizable published figures)

include (Figure 22): North Carolina (NCSM/IMS; Bush, 1885a, b; Dall, 1886, 1889; Maury, 1920; Johnson, 1934; M. Smith, 1937, 1941, 1945, 1951; Aguayo & Jaume, 1950; Abbott, 1954, 1974; Morris, 1973; Porter, 1974; Porter & Wolfe, 1971; Merrill et al., 1978; Abbott & Morris, 1995); South Carolina (NCSM/IMS; Porter, 1975); Georgia (NCSM/IMS; Dall, 1889); Florida, off eastern coast from St. Lucie County to Miami (AMNH, ANSP, FMNH, HBOM; McGinty & Nelson, 1972; Lyons, 1989; Lee, 2000), and the Florida Keys (AMNH, ANSP, HMNS, SBMNH, FK stations [Table 1]; Dall, 1881; Vittor, 1998); Gulf of Mexico, off western Florida from Boca Grande through Destin (Florida panhandle) (AMNH, ANSP, DMNH, FMNH; Maury, 1920; Gundersen, 1998), Alabama (HMNS; Shelton, 1997), Mississippi (Bock & Moore, 1968), Louisiana (ANSP, HMNS), Texas (HMNS; Odé & Spears, 1970; Treece, 1979); the Bahamas (AMNH), Guadeloupe (BMNH 1854.10.4.550 [types]; d'Orbigny, 1853), and Yucatan (Dall, 1881; Vokes & Vokes, 1984). Localities that have not been verified are: Virginia (Merrill et al., 1978), Cuba (d'Orbigny, 1853; Dall,



Figures 18–21. *Varicorbula disparilis*, details of anatomy, scanning electron micrographs of critical-point dried animals. Figure 18. Siphons; excurrent (dorsal) at upper right. Figure 19. Foot. Figure 20. Gills (posterior at left). Figure 21. Gill filaments. Scale bars = 20 μm (21), 200 μm (18, 19, 20).

1881, 1885, 1886; McLean, 1936; M. Smith, 1940; Aguayo & Jaume, 1950; Espinosa et al., 1994), Dominican Republic (Dall, 1885), Virgin Islands (Dall, 1881), Barbados (Dall, 1881), Martinique (d'Orbigny, 1853), Venezuela (Aguayo & Jaume, 1950), and Barbados (Dall, 1886, 1889; Maury, 1920). *Varicorbula disparilis* has likewise not been verified from Puerto Rico (Dall & Simpson, 1901; McLean, 1951; Warmke & Erdman,

1963) or Jamaica (d'Orbigny, 1853); all specimens seen thus far from Puerto Rico (AMNH, ANSP; Warmke & Abbott, 1961: text-fig. 31h) and Jamaica (AMNH, ANSP, DMNH, MCZ; C. B. Adams, 1852; Cockerell, 1894) are *V. krebsiana* (see below). Likewise, all known records from Grand Cayman (ANSP; Abbott, 1958), the Dominican Republic (AMNH), Haiti (E. A. Smith, 1885), the Virgin Islands (DMNH; Weber, 1961), Bermuda (DMNH;

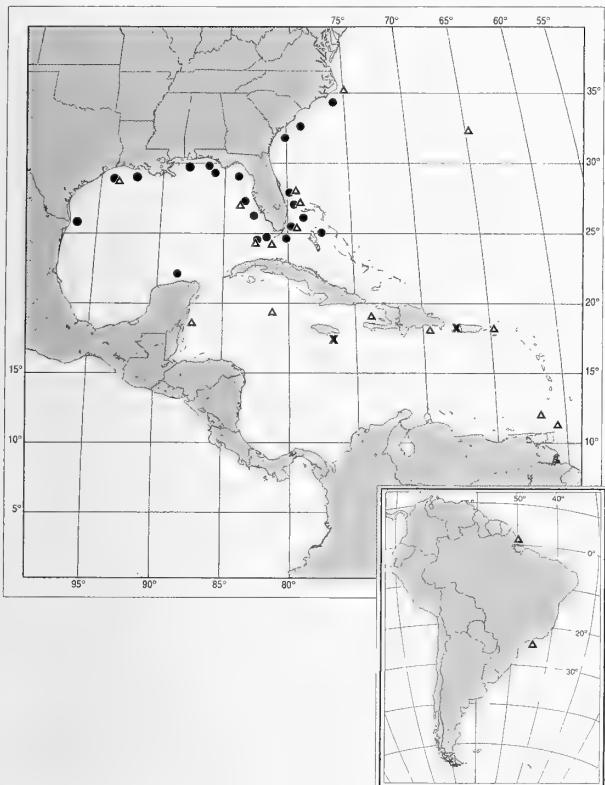


Figure 22. Verified geographical distribution of *Varicorbula disparilis* (solid circles), *V. krebsiana* (x, Jamaica and Puerto Rico only), and *V. philippii* (open triangles).

E. A. Smith, 1885; Dall, 1889; Aguayo & Jaume, 1950; Waller, 1973; Jensen & Harasewych, 1986), and Brazil (Aguayo & Jaume, 1950; Rios, 1975, 1985, 1994) are *V. philippii* (see below). One published figure of a *Varicorbula* in the western Atlantic literature appears entirely incorrect: Morris' (1973: pl. 31, fig. 8) illustration of *Notocorbula operculata* shows an equivalve clam with no recognizable sculpture.

In summary, according to the known species distributions thus far, *Varicorbula disparilis* borders the continental coastline of the eastern United States and Gulf of Mexico. Although *V. philippii* overlaps much of this range (see below), it is also found in Bermuda and Caribbean locations (Belize, Greater and Lesser Antilles, Brazil). *Varicorbula krebsiana* is so far restricted to Jamaica and Puerto Rico.

Ecology: *Varicorbula disparilis* can be classed as a relatively deep-water continental-shelf species with recorded depths often exceeding 200 m (AMNH; Dall, 1881:127 and 450 fms = 232 and 823 m; Dall, 1881, 1886, 1889: 805 fms = 1473 m; Merrill et al., 1978: 475 m; Abbott, 1974:250 fms = 457 m). However, its range of depth is notable (Humfrey, 1975); very shallow depths (< 10 m) have also been recorded (Dall, 1889: 5 fms = 9 m; Mer-

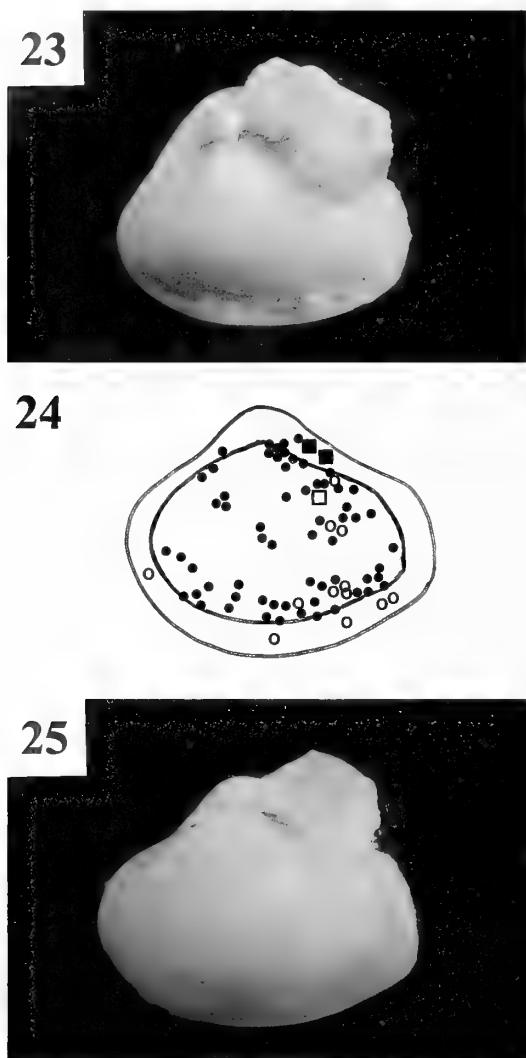
rill et al., 1978: 9 m; Lyons, 1989: 7.1 m). Collections verified as live-collected are from 16.5–91.5 m (AMNH, HBOM, HMNS, NCSM/IMS; FK stations [Table 1]; Porter, 1975). Bottom type is either sand or mud (NCSM/IMS; FK stations [Table 1]; Porter, 1975). It has been recorded from the gut contents of bottom-feeding starfish (*Astropecten duplicatus* Gray, 1840) off North Carolina (Porter & Wolfe, 1971; as *V. operculata*, vouchers NCSM-IMS), and bottom-feeding bonefish [*Albula vulpes* (Linnaeus, 1758)] off Puerto Rico (Warmke & Erdman, 1963; as *Notocorbula operculata*, unverified).

Corbulids are well known for organic conchiolin layers within the matrix of the calcareous shell, presumably protecting the bivalve from chemically boring predators and shell dissolution in deep and/or cold calcium-carbonate-deficient waters (Lewy & Samtleben, 1979; Morton, 1990; although Anderson et al. [1991] showed that other factors [e.g., size] might be more important against predation). Both complete and incomplete boreholes have been noted in the material examined herein (FK-98, FK-104; AMNH 273274, HMNS 7345). Some of these boreholes are distinctly bevelled, while others are straight-sided, suggesting several predator species (e.g., Naticidae, Muricidae). The conchiolin layer has also been viewed as a "gasket" to seal the edge of the smaller left valve into the groove of the larger right valve, to the extent that presence of the internal groove alone was interpreted as evidence of conchiolin in fossilized species by Lewy & Samtleben (1979).

Population structure: Thirty-five living specimens were obtained in the FK-104 Shipek grab sample. Based on the grab's surface area of ca. 1 ft² (=0.093 m²), population density at this location can be estimated at 376 individuals/m². Within this quantitative sample, shell length of the larger right valve ranged from 4.8 to 7.8 mm (mean = 6.4 ± 0.7 SD, n = 35). A random sample of specimens from the trawl sample (FK-106) was similar (range 4.6–8.7 mm, mean = 6.7 ± 0.8 SD, n = 65).

The catch of the trawl sample (FK-106) was limited to common shallow water fishes and crustaceans. The "tickle chain" sample contained an estimated 3200 living specimens of *Varicorbula disparilis* entangled within the mat. Also present were a few living individuals of mussels (*Amygdalum politum* Verrill & Smith, 1880), single living specimens of the jingle shell (*Anomia simplex* d'Orbigny, 1842) and a second corbulid (*Corbula caribaea* d'Orbigny, 1842), plus empty shells of various bivalves [*Gouldia cerina* (C. B. Adams, 1845), species of *Nuculana*, *Anadara*, Tellinidae, and Lucinidae], gastropods [*Acteocina bidentata* (d'Orbigny, 1842), species of *Calyptaea*, *Olivella*, Turridae, and Pyramidellidae], and fragments of sea urchins and barnacles.

Numerous *Varicorbula* specimens in FK-106 served as substratum to other attached mollusks (Figures 23–25). The most common is a species of Arcidae (2.6–6.1 mm,



Figures 23–25. *Varicorbula disparilis*, FK-106, specimens with attached mollusks. Figure 23. *Anadara* cf. *floridana*, attached to a 7.0 mm *V. disparilis*. Figure 24. Distribution of attached mollusks ($n = 75$) on *V. disparilis* shells ($n = 41$). Solid circles = *A. cf. floridana* (or its byssus); solid squares = *Arcinella cornuta*; open circles or squares = attachment of respective attached mollusks on other side of shell. Figure 25. Neologic *A. cornuta*, attached to a 7.2 mm *V. disparilis*.

mean 4.1 ± 1.1 SD, $n = 10$; Figure 23), byssally attached to the *Varicorbula* most often (82%) on the smaller left valve. Distribution of attachment (evidenced by attachment site of byssal threads [$n = 72$] on 38 individual *V. disparilis*; maximum six attachments/clam) was more often on the posterior dorsal or ventral quadrants, but also occurred near the anterior end and at the center of the valves (Figure 24, circles). Larger empty specimens (up to 25 mm shell length) of this same form were also collected in most of the Shipek grabs listed in Table 1. The arcid species is clearly a member of *Anadara*—inequivalve,

moderately compressed, with a long straight hinge line, dark periostracum (hairy between the ribs, in dark concentric bands posteriorly), ca. 30 radial ribs (nodulose anteriorly), and a median radial indentation in the very early growth stage. Of the western Atlantic species, it is closest to *Anadara floridana* (Conrad, 1869), although that species has a much larger “adult” size (8–10 cm) which has not been collected or otherwise seen from the Florida Keys in this study.

Three other *Varicorbula* specimens each have a small (2.1–3.3 mm, mean 2.7 ± 0.5 SD) attached specimen of a species of Chamidae (Figure 25), barely past the prodissoconch stage. The chamid’s prodissoconch is smooth, orange or cream (one with radial pink rays), with widely spaced, thin, raised concentric ridges. The first growth of teleoconch has ruffled sculpture. Attachment to *Varicorbula* is near the posterodorsal hinge line (Figure 24, squares), cemented by the right valve of the chamid. By comparison with very small specimens of other western Atlantic Chamidae species, the form is attributable to *Arcinella cornuta* Conrad, 1866 (e.g., FMNH 164927, Gulf of Mexico, dredged, 1962 Smith!, Goodwin Collection #1869, 2 specimens; see also Nicol, 1952:figs. 1–12, as *Echinochama*), a species also known from off eastern Florida, Key Largo, the Lower Florida Keys, the Gulf of Mexico, and the West Indies.

Byssal mat: The mat which entangled the clams to the trawl’s “tickle chain” was composed of byssus fibers plus long gelatinous egg strings covered with sand grains and shell fragments, along with filamentous algae and branching Bryozoa. The *Varicorbula* clams were byssally attached to the mat material when collected. Some byssal threads reached several times the shell length. The egg string is tubular, round in cross-section, 0.5 mm in diameter (after preservation), containing two rows (or a very tight coil?) of eggs, each in more or less spherical capsules (160–190 μm in diameter, not interconnected by chalazae), 115–125 per cm. All eggs were at in the same stage of development (unshelled, multicellular).

This mat of byssal threads and egg strands with which so many specimens of *Varicorbula limatula* were collected could be interpreted as a byssal “nest” (although none of the smaller Shipek grab samples confirmed this). While other bivalves are known to produce byssal mats (e.g., certain mytilids and limids; Thorsen, 1935; Fisher, 1936; Merrill & Turner, 1963; Morton, 1974), these typically encase the clam against a solid substratum. Byssal nests are thought to provide special protection to a thin-shelled adult, or to brooded larvae (Merrill & Turner, 1963); in *Varicorbula*, heavy byssal production, even though non-enveloping, could serve to more firmly anchor epibenthic individuals to rubble or sand particles (as in *Musculista*; Morton, 1974). It seems certain that more byssal production was involved here than a single byssal

thread per clam, attached to a below-sediment particle, as depicted for *V. gibba* by Stenzel et al. (1957:fig. 6).

It was initially tempting to speculate that the egg strands collected in the FK-106 sample were those of *Varicorbula disparilis*. A few other bivalve species are known to produce eggs in external strands or capsules [e.g., *Musculus discors* (Linnaeus, 1767), *Turtonia minuta* (Fabricius, 1780); see Thorson, 1935; Oldfield, 1955, 1964]. However, the available data for these egg strands and *V. disparilis* are inconclusive: (1) the encapsulated larvae were unshelled at the time of collection; (2) despite repeated trials, staff in the AMNH Invertebrate Molecular Systematics Laboratory were unable to extract DNA from the eggs for comparison with that of the adult clams (probably due to inadequate preservation; G. Giribet, personal communication); (3) multicelled embryos in the egg strands are 170 µm diameter (prodissococonch I is 200 µm diameter); eggs in ovarian follicles of the single sectioned female are a magnitude smaller (16–20 µm diameter), but this could merely indicate an early developmental stage (Morse & Zardus, 1997); and (4) no accessory glandular structures were found in sectioned specimens (such as the thickened mantle edges postulated to secrete the saclike egg capsules in *T. minuta*; Oldfield, 1955, 1964). Other mollusks occurring in the area are known to produce superficially similar egg strands (most especially, *Strombus* spp.; Robertson, 1959), and we cannot rule these out as the source. The association of *V. disparilis* with this benthal/egg mat is nevertheless intriguing, and is presented here for future reference.

Varicorbula krebsiana (C. B. Adams, 1852)

(Figures 22, 26)

Selected synonymy:

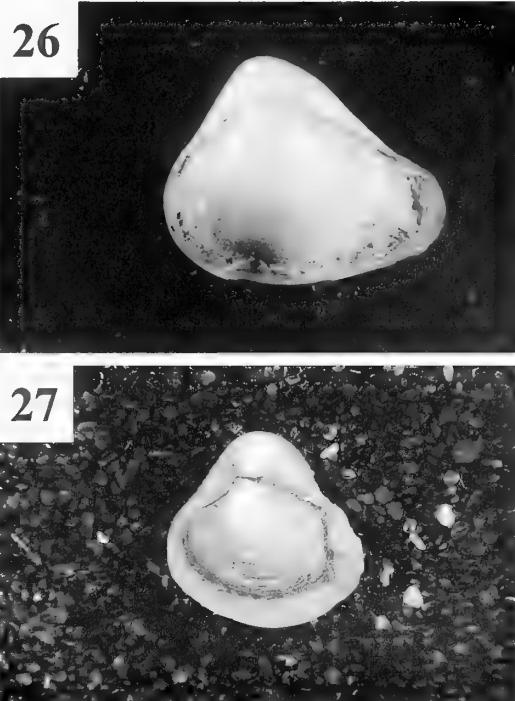
Corbula krebsiana C. B. Adams, 1852:234. Type locality: Jamaica.—Dall, 1886: 315, 316, pl. 1, figs. 1, 1a, b; 1889:70, 71, pl. 1, figs. 1, 1a, b [after Dall, 1886].—Clench & Turner, 1950:300, pl. 48, fig. 3.—Abbott, 1974:539, text-fig. 6011 [after Dall, 1886].

Corbula krebsiana C. B. Adams.—M. Smith, 1937:67, pl. 60, figs. 1a, b [after Dall, 1886]; 1940:120, sp. 1559, figs. a, b [after Dall, 1886]; 1941:67, pl. 60, figs. 1a, b [after Dall, 1886]; 1945: 67, pl. 60, figs. 1a, b [after Dall, 1886]; 1951: 67, pl. 60, figs. 1a, b [after Dall, 1886].

Notocorbula operculata Philippi, 1848 [sic].—Warmke & Abbott, 1961: text-fig. 31h.

Diagnosis: *Varicorbula* of 3–5 mm shell length. Radial ridges on left valve weak. Truncation:height ratio (= height of truncated posterior edge of right valve versus total dorsoventral height) 35–39%.

Remarks: *Corbula krebsiana* C. B. Adams, 1852, described from Jamaica, is very similar to *Varicorbula disparilis*, including in coloration ("often tinged with pink";



Figures 26, 27. Figure 26. *Varicorbula krebsiana*, MCZ 115611, Jamaica, lectotype, 6.1 mm length. Figure 27. *Varicorbula philippii*, AMNH 128166, off Palm Beach County, Florida, 6.4 mm length.

C. B. Adams, 1852:234). It was placed in synonymy with *V. operculata* by Rios (1970, 1975, 1985, 1994), without further explanation; C. B. Adams (1852:234) stated that it "probably . . . resembles *C. operculata* Phil." and Andrews (1981a, b, 1992, 1994) listed it as a possible synonym. The type specimens of *C. krebsiana* (lectotype: MCZ 155611 [Dall, 1886:pl. 1, figs. 1, 1a, b; right valve only figured by Clench & Turner, 1950:pl. 48, fig. 3; Figure 26]; paralectotypes: MCZ 155612, DMNH 21941, ANSP 297148, ANSP 182624; see also Mikkelsen & Bradford, 1997) are overall smaller and more posteriorly pointed than typical *V. disparilis*. That is, in comparably sized specimens (3–5 mm length), the truncation:height ratio is smaller in *C. krebsiana* (35–39%, n = 4; also evident in illustrations by Dall [1886: pl. 1, figs. 1, 1a, b], and Warmke & Abbott [1961:text-fig. 31h]) than in *V. disparilis* (42–46%, n = 4). Dall (1886) maintained it as distinct on the basis of its "more delicate" (= smaller) form; others (Tryon, 1869, with "?"; Cockerell, 1894; Johnson, 1934; Lamy, 1941; M. Smith, 1937, 1941, 1945, 1951; Weisbord, 1964; Abbott, 1974; Odé, 1976) have agreed. In the absence of additional evidence, we maintain this species as valid within *Varicorbula* pending further data.

Although Dall (1889) included Cape Florida and the Florida Keys in its distribution (also M. Smith, 1937,

1940, 1945; Aguayo & Jaume, 1950; Abbott, 1974), we have seen specimens only from Jamaica (AMNH, ANSP, DMNH, MCZ) and Puerto Rico (AMNH, ANSP, FMNH) (Figure 22). Warmke & Abbott's material from Puerto Rico, based on their illustration (Warmke & Abbott, 1961:text-fig. 31h, as *Notocorbula operculata*), appears to be *V. krebsiana*; other Puerto Rican records (Dall & Simpson, 1901; Warmke & Erdman, 1963) cannot be verified in the absence of an illustration or voucher material. Its occurrence in Cuba (Aguayo & Jaume, 1950) is also unverified. Its depth range is usually deep, although shallow-water collections have also been noted (Dall, 1889: 3–85 fms [5.5–155.5 m]; this study 5.5–7 m [MCZ]); none of these records is, however, based on verified living populations.

Varicorbula philippii (E. A. Smith, 1885)

(Figures 22, 27)

Selected synonymy:

- Corbula philippii* E. A. Smith, 1885:33–34, pl. 8, figs. 4–4b.
Aloidis operculata (Philippi, 1849 [sic]).—Pulley, 1953: 197–198, pl. 18, fig. 17.
Corbula (Varicorbula) operculata Philippi, 1849 [sic].—Rios, 1975:251, pl. 80, fig. 1205; 1985:270, pl. 94, fig. 1334; 1994:292, pl. 99, fig. 1427.
Corbula (Varicorbula) operculata (Philippi, 1849 [sic]).—Andrews, 1981a:140, text-fig.; 1981b:140, text-fig.; 1992:140, text-fig.; 1994:145, text-fig.
Varicorbula operculata (Philippi).—Jensen & Harasewych, 1986:488–489, fig. 162.
Varicorbula operculata (Philippi, 1848).—Abbott & Morris, 1995:pl. 23, fig. 11 top specimen only (color).—Vokes & Vokes, 1984:pl. 47, figs. 7a, b only.
Corbula krebsiana C. B. Adams, 1852.—Andrews, 1971: 216–217, text-figs.
Corbula cf. krebsiana C. B. Adams, 1852.—Andrews, 1977: 251, text-figs.

Diagnosis: *Varicorbula* of 5–9 mm shell length. Periostracum thick; radial ridges on left valve strong, extending nearly from margin to umbo. Truncation:height ratio (= height of truncated posterior edge of right valve versus total dorsoventral height) 46–52%.

Remarks: *Corbula philippii*, described from Bermuda and Haiti, was included in synonymy with *C. disparilis* [and/or *Varicorbula operculata*] by a number of authors (Dall, 1886; Guppy & Dall, 1896; Lamy, 1941; Aguayo & Jaume, 1950; Pulley, 1953; Anderson, 1996), but is distinct according to the original description and material examined herein. It reaches overall shell lengths equal to those of *V. disparilis*. The radial periostracial ridges on the smaller left valve (Figure 27) are more pronounced than in *V. disparilis* or *V. krebsiana*, and extend nearly up to the umbo. The larger right valve is heavier and more inflated, and has a more pronounced posterior ridge, as well as a more strongly squared posterior truncation.

The truncation:height ratio is greater (46–52%, n = 6) than that in either *V. krebsiana* or *V. disparilis*. As in the case of *V. krebsiana*, this species is provisionally maintained as distinct within *Varicorbula* pending further data. It overlaps in distribution (Figure 22) with *V. disparilis* off North Carolina (NCSM/IMS), the eastern and western coasts of Florida (AMNH, ANSP, DMNH, FMNH, HBOM, HMNS; Andrews, 1994) and off Texas (HMNS; Andrews, 1971, 1977, 1981a, b, 1992), and is also recorded from Bermuda (DMNH; Jensen & Harasewych, 1986), Grand Cayman Island (ANSP), the Dominican Republic (AMNH), the Virgin Islands (DMNH), Grenada (ANSP), Tobago (ANSP), and Belize (ANSP). Based on published figures alone (Rios, 1975, 1985, 1994; Vokes & Vokes, 1984), it also occurs in Brazil (Amapá to Rio de Janeiro) and Yucatan. Lamy (1941:219) also mentioned specimens from Martinique which “bien conforme aux figures de Smith,” thus apparently *V. philippii*. Andrews (1981a, b, 1992, 1994; as *C. krebsiana* or *C. operculata*, but figuring *V. philippii*) reported its occurrence off Texas in bamboo-root clumps, commensal with foraminiferans. A similar habit off Texas was earlier noted by Odé & Spears (1970:71; as *Notocorbula operculata*, but identity unverified) as “the attachment root of whip-coral” (see also Odé, 1965) and “in rootmasses washed ashore.” It has been recorded (along with *V. disparilis*, see above) from the gut contents of bottom-feeding starfish (*Astropecten duplicatus*) off North Carolina (Porter & Wolfe, 1971; as *V. operculata*, vouchers NCSM-IMS).

Complete and incomplete boreholes (as described for *Varicorbula disparilis* above) were also noted in specimens of *V. philippii* (AMNH 94733, 248383, 248935, HMNS 7345). One still-articulated specimen of *V. philippii* (HMNS 7345) had five boreholes, three on the larger right valve, and two (including the successful complete one near the umbo) in the smaller left valve.

DISCUSSION

Varicorbula species, either alive or as empty shells, comprise some of the most common bivalved mollusks in benthic samples from the continental shelf of the tropical western Atlantic. Although they were formerly lumped under a single species name, *V. operculata*, this study has recognized the at-least-conchological existence of three separable morphospecies (*V. disparilis* [= *V. limatula*], *V. krebsiana*, *V. philippii*), while ironically relegating the most common species name, *V. operculata*, to the status of *nomen dubium*. Distinguishing shell characters for the three species are summarized in Table 2.

Anatomical data for members of the family Corbulidae are scanty. Those of *Varicorbula gibba*, type of the genus, were described by Yonge (1946); those of *V. disparilis* are described here. The only other genus known anatomically is *Corbula*, exemplified by *C. crassa*, presented by Morton (1990). Uniformity of non-shell char-

Table 2

Distinguishing characters and confirmed distribution of the three western Atlantic species of *Varicorbula*.

	<i>V. disparilis</i>	<i>V. krebsiana</i>	<i>V. philippii</i>
Shell length	5–9 mm	3–5 mm	5–9 mm
Radial ridges on left valve	moderate, margins only	weak	strong, margin to umbo
Periostracum	moderate	moderate	thick
Truncation : height ratio	42–46%	35–39%	46–52%
Distribution (confirmed)	North Carolina, South Carolina, Georgia, Florida, Alabama, Mississippi, Louisiana, Texas, Bahamas, Guadeloupe, Yucatan	Puerto Rico, Jamaica	North Carolina, Florida, Texas, Grand Cayman Island, Dominican Republic, Haiti, Virgin Islands, Martinique, Grenada, Tobago, Belize, Yucatan, Brazil, Bermuda

acters from these three species in two presumed genera lends little support for such characters at the generic level. At the present time, shell characters remain the most important source of characters for defining genera and species within Corbulidae. Because of this paucity of available data, any phylogenetic analysis is premature and is not attempted here.

Varicorbula has been most often placed in the subfamily Corbulinae Gray, 1823 (Keen, 1969; Anderson, 1996) or Caryocorbulinae Vokes, 1945 (Vokes, 1945; Olsson & Harbison, 1953). However, at least two species of *Varicorbula* (the type species, *V. gibba*, and *V. disparilis*; Yonge, 1946, and this study, respectively) have calcification of the marginal siphonal periostracum in the left valve of some specimens. In this respect, *Varicorbula* agrees with the subfamily Caestocorbulinae Vokes, 1945, as originally defined. Although the siphonal calcification in recognized members of this subfamily (e.g., *Caestocorbula* Vincent, 1910, and *Parmicorbula* Vokes, 1944) is more elaborate than in members of *Varicorbula*, the latter agree in all other conchological features with this subfamily and its type genus (shell inequivalve, valves discrepant, left valve less rostrate, left valve with projecting chondrophore, left valve with weaker concentric sculpture and with radial ornamentation, right valve grooved for reception of left valve; Vincent, 1910; Vokes, 1944, 1945). *Notocorbula vicaria* also has been reported with siphonal calcification (Martin, 1918) and may also warrant reclassification to this subfamily. Placement of *Varicorbula* in Caestocorbulinae would extend the paleontologic range of this subfamily from the Cretaceous (Vokes, 1945) to the Recent.

Published accounts of life habits in members of the family Corbulidae (Yonge, 1946; *Varicorbula gibba*; Morton, 1990; *Corbula crassa*; Stanley, 1970; *C. caribaea*) have described very slow-burrowing animals, living close to the surface-sediment interface (reflected by the very short siphons), along with occasional above-surface attachment. Bock & Moore (1968:274) reported that *V. disparilis* (as *Notocorbula operculata*), along with its attached commensal foraminiferan, “climb[ed] above the

flocculent layer close to the bottom” by baysally attaching to *Chaetopterus* worm tubes. The available evidence from these collections, especially the method of capture and apparently random location of attached epifaunal mollusks, agrees with Bock & Moore (1968) by suggesting that *V. disparilis* is more epifaunal/epibyssate than infaunal/endobyssate. Whether *V. disparilis* lives a strict epifaunal existence or one among the fragments of coarse “shell hash” is equally undetermined; it is clear that *V. disparilis* in this instance was not buried into finely grained sand or mud. The inequivalve shell and relatively small foot of *V. disparilis* also suggest limited burrowing ability.

Lamprell et al. (1998:366) noted that corbulids often “occur in large numbers in their preferred habitat” (also noted for fossil assemblages by Stenzel et al., 1957) and cited examples of species of *Notocorbula* that are “known to be gregarious.” *Varicorbula gibba* exists in densities up to 600 individuals/m² in the northern Adriatic Sea (Hrs-Brenko, 1981); interestingly, the highest numbers were recorded in polluted harbors. High numbers are also well recorded in the fossil record as corbulid-dominated assemblages (summarized by Lewy & Samtleben, 1979). *Varicorbula disparilis* encountered during this study also existed in large numbers, often as the only living mollusk found in Shipek grab samples, and in a nearly monocultural situation in the dredged byssal mat.

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Microhabitat Segregation of Co-Existing Gastropod Species

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Abstract. The formation of aggregations of four co-existing species of nerite gastropod was investigated on a tropical rocky shore in north Queensland, Australia. The results demonstrated that all species formed mono-specific aggregations, each of which had a strong fidelity for aggregating within a particular microhabitat type. Hence there was a distinct segregation of microhabitat usage among the four co-existing, ecologically similar species, and this segregation did not differ spatially or temporally. These results indicate that spatial and temporal fluctuations of abiotic conditions had little impact on the formation of aggregations, and that factors such as competition for microhabitats among species may play a greater role in the formation and maintenance of intertidal gastropod aggregations than previously thought.

INTRODUCTION

During periods of emersion, many intertidal rocky shore gastropods form multi-layered aggregations or clumps within particular microhabitats such as cracks/crevices in the rock surface. For species of the genus *Nerita* Linnaeus, 1758, there is considerable evidence (see Vermeij, 1973; Vannini & Chelazzi, 1978 and references therein; Garrity, 1984; Garrity & Levings, 1984) supporting the notion that aggregating behavior assists in alleviating the potentially lethal increases in temperature, and associated risks of desiccation, to which intertidal rocky shore gastropods are subject during low tides, particularly during summer.

The degree to which different species exhibit aggregation behaviors is dependent on local environmental conditions. For any one species, the prevalence of aggregations, and the intertidal distribution of those aggregations, will be dependent upon local patterns of water movement and availability of food (Rohde & Sandland, 1975; Vannini & Chelazzi, 1978; Branch, 1981); presence of conspecifics (Chapman, 1999; Davies & Bechwith, 1999); size of any individual animal within the population (Levings & Garrity, 1983; Chelazzi et al., 1984, 1985), and aspects of the habitat (Rohde & Sandland, 1975; Rafaelli & Hughes, 1978; Vannini & Chelazzi, 1978; Branch, 1981; Garrity & Levings, 1984; Chapman & Underwood, 1994; Crowe & Underwood, 1998). However, it remains to be seen whether aggregation behaviors are affected by seasonal fluctuations in abiotic conditions.

The formation of aggregations is facilitated by each species' ability to utilize direct visual cues (Vannini & Chelazzi, 1978; Chelazzi & Vannini, 1980) and by their ability to detect and follow substrate markings present in the mucus trails of conspecifics (Cook 1969, 1971; Chelazzi et al., 1983; Raferty, 1983; Gilly & Swenson, 1978; Chapman, 1999; Davies & Bechwith, 1999). By having

a strong homing preference and following conspecific mucus trails, species do not occupy suitable sites at random but show a strong affinity for aggregating in particular microhabitats through time (Chelazzi et al., 1985). Although the formation of conspecific aggregations and their affinity for particular microhabitats has been recorded in *Nerita textilis* Gmelin, 1791 (Chelazzi et al., 1985 and references therein), the generality of this microhabitat loyalty across other species of *Nerita* is unknown.

Furthermore, it is also unknown whether the presence of more than one species of *Nerita* within a habitat affects the homing behavior of individual species and therefore influences the aggregation behavior of individuals within the population. Just as intraspecific competition affects the layering of individuals within monospecific aggregations (Garrity & Levings, 1984), so too could interspecific competition affect the behaviors of co-existing ecologically similar species. Each species may utilize unique aggregation cues and therefore form monospecific aggregations. Alternatively, aggregation cues may be the same among closely related species, which could result in a number of species aggregating together.

This study was carried out on a sheltered rocky shore in north Queensland where four nerite species co-exist in the mid and lower intertidal regions (unpublished data). The microhabitats in which these species aggregate during periods of emersion include the vertical surfaces of rocks, around the base of rocks, and within cracks and crevices on the rock surfaces. The specific aims of this study were to determine (1) whether aggregations within these microhabitats were mono-specific or if they consisted of a mixture of species; (2) whether any particular species was consistently found to occur in only one microhabitat type; (3) whether there was any difference in the structure of the aggregations formed in the low and mid-intertidal regions; and finally (4) whether there was

any temporal (between summer and winter) consistency in the observations made.

METHODS

Study Site

This study was carried out on a sheltered rocky shore in Townsville, north Queensland, Australia ($19^{\circ}11'S$, $146^{\circ}46'E$). The intertidal topography of the shore varies considerably; large granite outcrops are prominent within the upper intertidal regions (above Mean High Water Neap, MHWN) but graduate into a boulder field below MHWN. Boulders vary in size from < 0.5 m up to approximately 2 m across the long axis.

The surfaces of boulders are fissured by cracks and crevices. For this study a crack was defined as a fissure in the rock surface which measured greater than 20 cm long, 5 cm wide, and 2 cm deep. A crevice was defined as a fissure in the rock surface which also measured greater than 20 cm long, but less than 5 cm wide and 0.5 cm–2 cm in depth. Although these microhabitats are quite similar, a distinction between them is necessary, as the differing depths and widths of each would result in different water retention capabilities within each microhabitat. Because decreasing the risk of desiccation is a strong force driving aggregation behaviors of tropical nerites (Vannini & Chelazzi, 1978 and references therein; Garrity, 1984; Garrity & Levings, 1984), the difference between these microhabitats may affect the frequency of use of either microhabitat by members of the nerite population inhabiting this shore.

Sampling Design

During periods of emersion, individuals of *Nerita chamaeleon* Linnaeus, 1758, *N. costata* Gmelin, 1791, *N. polita* Linnaeus, 1758, and *N. undata* Linnaeus, 1758, were typically observed forming multilayered aggregations in any of four microhabitats on the boulder surfaces: (1) cracks or (2) crevices present on the surfaces of the boulders, or on (3) the vertical surfaces, or (4) around bases of boulders at the rock-sand interface.

To examine whether or not the aggregations within any of these four microhabitats were mono-specific, 40 boulders greater than 1 m wide, and on which all four microhabitats were present, were identified from both the mid and lower intertidal regions. Twenty boulders from each intertidal area were then randomly selected from those 40. On each boulder I recorded the occurrence of species within one representative microhabitat of each of the four types. Hence, from both the mid and the lower intertidal regions I recorded the occurrence of species within 20 replicate cracks, 20 replicate crevices, 20 replicate vertical walls, and 20 replicate base areas.

In each microhabitat, samples were taken by laying a rectangular quadrat (10 cm wide \times 20 cm long) over a

microhabitat and recording the abundances of species which occurred within the quadrat. The use of a quadrat provided consistency of sampling effort among each microhabitat on the same boulder, and among boulders.

To determine whether there was any temporal consistency in the observations, sampling was first conducted during the summer (January) and again repeated during the winter (June) of 1997. As such, a total of 20 replicates were sampled from each microhabitat type in each intertidal region (2 of) on two different sampling occasions.

Statistical Analysis

To determine if there was any intertidal or seasonal difference in the average number of species present in a microhabitat type, an Analysis of Variance (ANOVA) was used. An ANOVA was also used to determine if there were any significant differences in the mean numbers of each species occupying mid and low intertidal levels between summer and winter. To examine the spatial and temporal variability of the compositions sampled within each of the four microhabitats non-Metric Multi-dimensional Scaling (nMDS), K-Means clustering ($K = 4$) and SIMPER analysis (Clarke, 1993) were applied to the average number of each species occurring within each microhabitat for the two spatial and temporal scales. Identification of whether any species had an affinity for a microhabitat type or an intertidal level was also achieved using SIMPER. Analyses were applied to raw data, and the Bray Curtis distance measure was used to calculate the dissimilarity matrix for the nMDS.

RESULTS

There were no significant differences in the average number of species occurring in each of the four microhabitats between summer and winter or between the mid and lower intertidal levels (ANOVA, $n = 16$, $df = 1$, $P > 0.743$, $P > 0.948$, respectively). Each microhabitat was typically occupied by only one species regardless of season or intertidal level (Figure 1).

For each species (across all microhabitats) the average number of individuals sampled from the mid and lower intertidal regions did not differ significantly (ANOVA, $n = 40$, $df = 1$, $P > 0.3$, $P > 0.575$, $P > 0.784$, $P > 0.471$ for *N. chamaeleon*, *N. costata*, *N. polita*, and *N. undata*, respectively). However, there were significant differences in the average number of individuals sampled on each trip for all species except *N. undata*. Significantly more *N. chamaeleon*, *N. costata*, and *N. polita* were sampled during summer than during winter (ANOVA, $n = 40$, $df = 1$, $P < 0.001$, $P < 0.05$, $P < 0.05$, respectively; Figure 2).

The relative abundance of species present within each microhabitat was distinct from that of any other microhabitat. This is seen by the separation of the composition and abundance information into microhabitat-specific

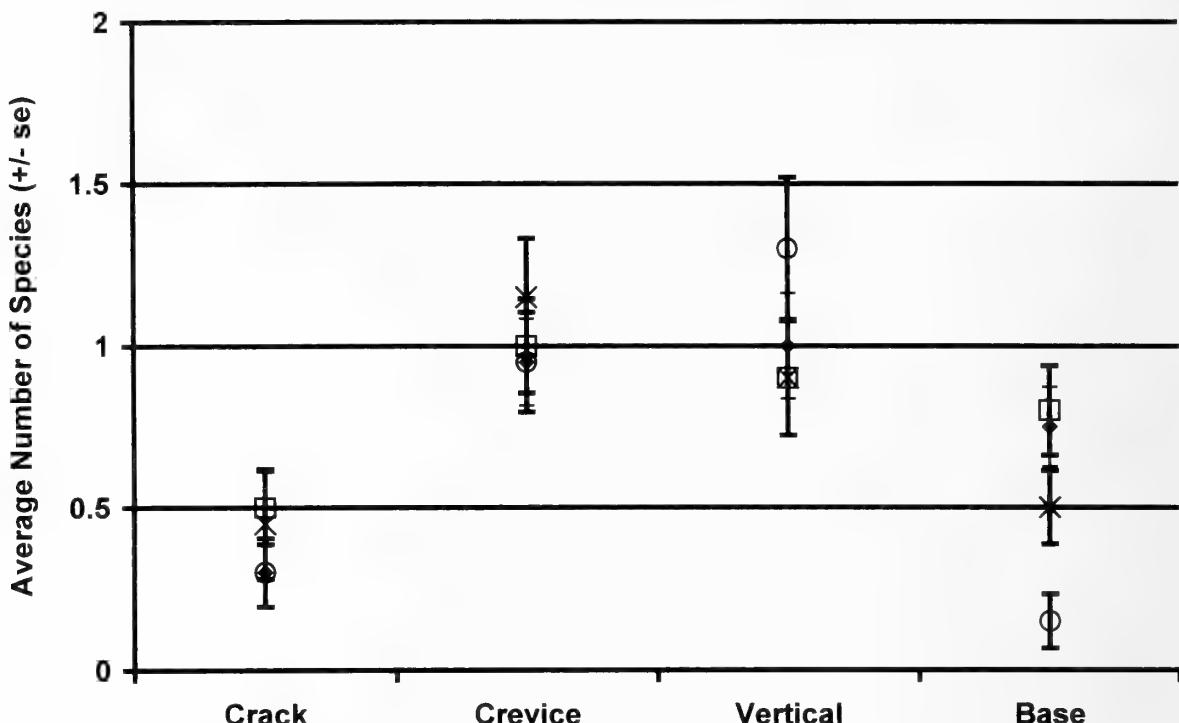


Figure 1. The average number of species occurring in each microhabitat (± 1 SE) in the mid and lower intertidal levels during summer and winter; (◆) mid intertidal level summer sample, (□) lower intertidal level summer sample, (*) mid intertidal level winter sample, (○) lower intertidal level winter sample.

clusters by the nMDS (Figure 3). However, within any one microhabitat the composition did not differ significantly between either intertidal level or season. The only exception was that the composition inhabiting cracks in the lower intertidal region during summer was most similar to that inhabiting crevices from both intertidal areas on both sampling occasions, as seen by the clustering of "sl crack" with all "crevice" samples on the ordination (Figure 3).

The relative contributions of each species, as determined by SIMPER analysis, to the structure of the ordination solution are shown in Table 1. This analysis indicates that *N. costata*, *N. polita*, and *N. undata* each had a strong affinity for a particular microhabitat. This is further supported by examining the relative contribution of each species to the total number of individuals found in each microhabitat (Figure 4). *Nerita costata* predominantly occupied the vertical surfaces of boulders, *N. polita* was typically found around the bases of boulders, and *N. undata* was mainly found in the crevices of boulder surfaces (Figure 4). Conversely, *Nerita chamaeleon* was present in consistent numbers in cracks and crevices, and was also found on the vertical walls, but not around the bases of boulders.

The affinity of each species for a different microhabitat regardless of season or intertidal level is responsible for the clear separation of the microhabitat types on the or-

dination (Figure 3). The clustering of "sl crack" with the "crevice" samples is due to the composition of cracks at this sampling time being most similar to the composition of crevices at any sampling time. During summer, both *N. chamaeleon* and *N. undata* were present in cracks in the lower intertidal region. However, in all other samples this microhabitat was typically only occupied by *N. chamaeleon*, whereas crevices were always occupied by both species. Although two species were found to occupy crevices, they did not cohabit in any one crevice, but each species formed mono-specific aggregations in separate crevices (Figure 1). No other spatial or temporal differences in the composition of each microhabitat were found. The dominance of each microhabitat by a particular species and the occurrence of *N. chamaeleon* in a number of microhabitats were consistent patterns between the two intertidal levels and between summer and winter.

DISCUSSION

The four species of nerite gastropods examined during this study each formed mono-specific aggregations on this shoreline. The formation of these mono-specific aggregations occurred in both the upper and lower intertidal regions and during both summer and winter. As such, this behavior was independent of any intertidal gradient and/or seasonal variability of abiotic conditions.

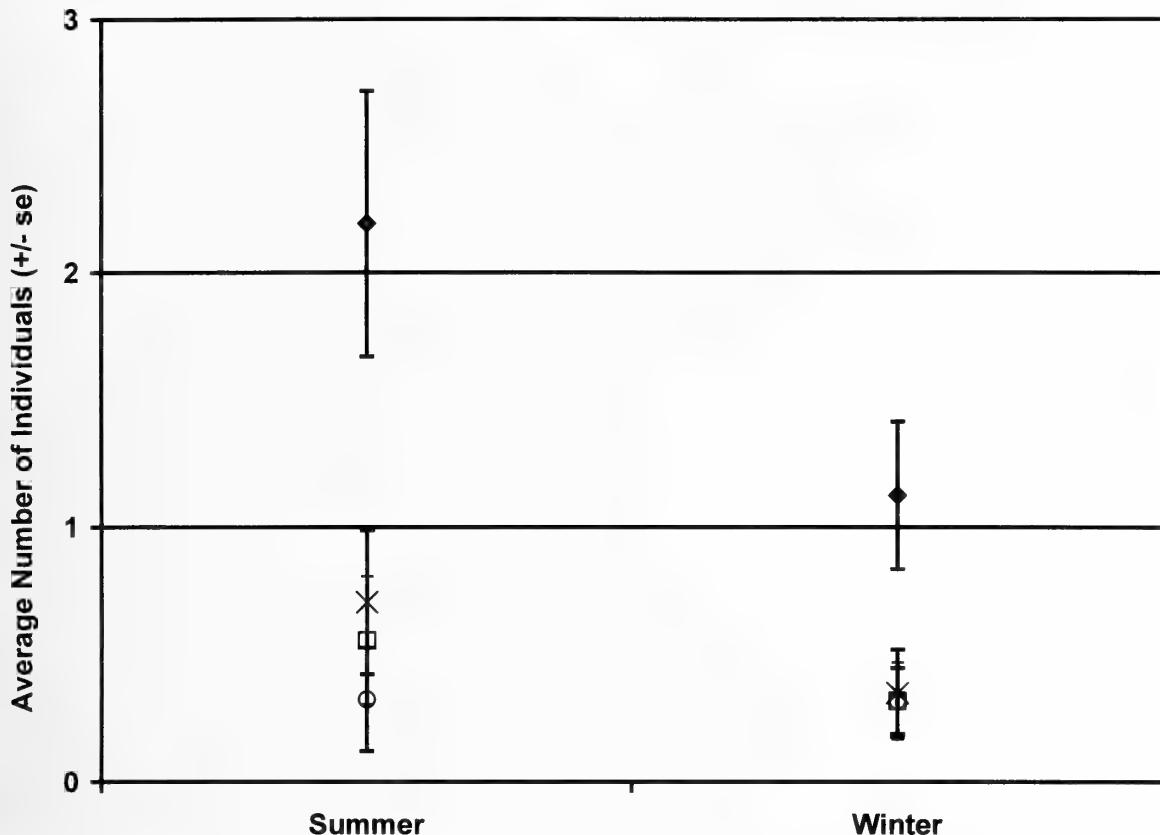


Figure 2. The average number of individuals (± 1 SE) of each species during summer and winter across all microhabitat types and both intertidal levels. (\blacklozenge) *Nerita chamaeleon*, (\square) *N. costata*, (\ast) *N. polita*, (\circ) *N. undata*.

Intertidal gastropods form aggregations to alleviate their exposure to potentially lethal abiotic stresses during periods of emersion (Moulton, 1962; Willoughby, 1973; Vermeij, 1973; Rohde & Sandland, 1975; Garrity & Levings, 1984). However, studies (e.g., Vannini & Chelazzi, 1978; Chelazzi et al., 1985) have not examined whether competition for aggregation sites between ecologically similar species affects the composition of aggregations. This study conclusively demonstrates that ecologically similar species do not aggregate together. Each of the four ecologically similar species studied here formed monospecific aggregations regardless of intertidal level or season. This suggests that while abiotic pressures may drive the need to form aggregations, biotic factors clearly play an important role in the formation of each species aggregation.

This suggestion is supported by the fact that three of the species studied preferentially aggregated in a particular type of microhabitat. *Nerita polita* occurred predominantly around the bases of boulders, *N. undata* was mainly found inhabiting shallow crevices in the boulder surfaces, whereas *N. costata* occurred only on the vertical surfaces of the boulders. Given the similarity between the crack and crevice microhabitats, it was not surprising that

N. undata occurred in both in some samples (summer, low intertidal). It was interesting to note that other species rarely occupied more than one microhabitat. *Nerita chamaeleon* was more of a generalist, aggregating in crevices and on vertical surfaces, but primarily within deep cracks in the rock surfaces. The loyalty of each species to these microhabitats was found within both the mid and lower intertidal regions and during both summer and winter periods.

Studies examining the formation of aggregations of intertidal gastropods have typically focused on the behavioral mechanisms individual species invoke to facilitate their aggregation ability (Garrity & Levings, 1984; Chelazzi et al., 1983, 1984, 1985; Crowe & Underwood, 1998). These studies have determined that species exhibit homing behaviors to favorable microhabitats by following substrate markers present in the mucus trails of conspecifics (Cook 1969, 1971; Chelazzi et al., 1983; Rafferty, 1983; Gilly & Swenson, 1978; Chapman, 1998, 1999; Davies & Bechwith, 1999) and/or by detecting characteristics of the substratum (Vannini & Chelazzi, 1978; Garrity & Levings, 1984; Underwood & Chapman, 1990; Crowe & Underwood, 1998). However, these studies have not examined the specificity of different mech-

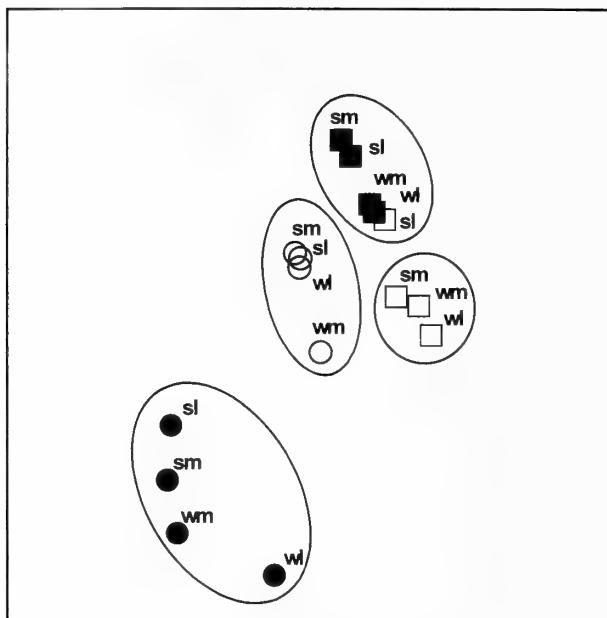


Figure 3. nMDS ordination indicating a difference in the composition of nerites occupying each of four microhabitat locations (□ crack, ■ crevice, ○ vertical wall, ● base of boulder). There were 20 replicates of each microhabitat sampled from the mid (m) and lower (l) intertidal regions during both summer (s) and winter (w). Stress = 0.04.

isms to particular species or genera nor have they determined if the presence or absence of competitive individuals affects aggregation behavior.

The formation of mono-specific aggregations within particular microhabitats regardless of any intertidal or seasonal variability of abiotic factors indicated that biotic factors may have a substantial influence on the formation and maintenance of aggregations for the species studied here. Furthermore, the results of this study, while not examining what process each species is using to form its aggregations, do clearly show that each species has a unique aggregation mechanism.

Given that space is one of the most limiting resources on rocky shores, particularly within the tropics (Lewis, 1964; Menge & Lubchenco, 1981; Garrity, 1984; Lubchenco et al., 1984), and that the four species examined here have similar ecological requirements, the fidelity of these species to particular microhabitats is most likely a response to competition, either current or historical, for aggregation sites. The aggregation cues each species utilizes may have evolved due to historical competitive pressures or may be an artifact of current competition for microhabitat space. The latter could be tested through a series of experimental manipulations whereby species are excluded from the habitat to determine if other species migrate into adjoining microhabitats.

In addition to the finding that there was no spatial variability in the preference of each species for particular

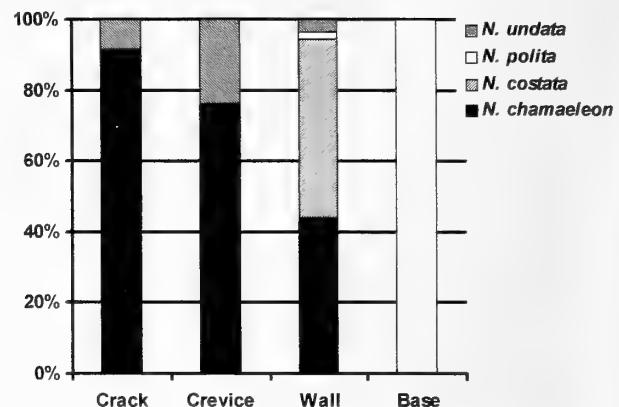


Figure 4. Percentage contribution of each species to the total number of individuals sampled from each microhabitat.

microhabitats, there were no significant differences observed in the abundances of species found in the aggregations across the intertidal gradient. The number of individuals aggregating did not differ between the mid and lower intertidal regions. To decrease their period of emersion, nerites have been shown to migrate down the shore in the wash of the falling tide (Vannini & Chelazzi, 1978; Garrity & Levings, 1981), and as a result, more individuals are usually found in lower intertidal regions during low tides. Given the harsh abiotic conditions on tropical rocky shores throughout the Indo-West Pacific (Lewis, 1964; Moore, 1972; Lubchenco et al., 1984), more individuals could be expected to occur at lower tidal levels. Conversely, the pressure to aggregate may decrease lower on the shore where conditions are less harsh; thus fewer individuals could be expected to occur in aggregations at lower tidal levels. As such, either an increasing or decreasing gradient of abundance could be expected. In this study no difference in the number of individuals aggregating across the intertidal gradient was detected. There are several possible explanations for this.

First, there may have been no difference in the abundance of individuals between the two areas because abiotic conditions differed little between the two areas. Alternatively, abundance may have differed between the intertidal regions, but the additional individuals were not in aggregations and were therefore not sampled during the

Table 1

Percentage contribution of each species of *Nerita* to the ordination solution as determined by SIMPER analysis.

	Crack	Crevice	Vertical	Base
<i>N. chamaeleon</i>	93	87	48	—
<i>N. costata</i>	—	—	45	—
<i>N. polita</i>	—	—	5	98
<i>N. undata</i>	—	12	2	—

study. However, observations do not suggest that the latter is the case. It is most likely that the abiotic conditions influencing this sheltered tropical shore do not differ markedly across the intertidal region. Under these conditions you would not expect any difference in the number of individuals found aggregating in each area, as seen here.

During summer periods, increases in temperature result in increased risks of thermal stress and desiccation (Moore, 1972; Williams, 1993). As temperature and desiccation stresses are extremely important determinants of the distribution of intertidal gastropod species (Vermeij, 1973; Underwood, 1979), the pressure to aggregate, and the number of individuals forming aggregations, would be expected to be greater during summer periods. During this study, significantly more individuals were seen to be aggregating in summer than in winter (Figure 2). This trend was observed for all microhabitats and across both intertidal regions. While it is possible that this pattern of behavior is a result of the increase in desiccation risk and thermal stresses during summer, it is unlikely, as solitary individuals not inhabiting one of the microhabitats examined were rarely observed prior to or during sampling.

In addition, the trend of more individuals being sampled during summer than winter occurred for all species except one, suggesting that the decline in abundance of individuals during winter was not due to species moving out of aggregations, but instead indicates an overall decline in the abundance of individuals occurring on the shore. This hypothesis is supported by the fact that a decline in abundance of all intertidal gastropod species inhabiting this area occurred during the winter sampling period (unpublished data).

In summary, the aggregations observed during this study generally comprised only one species. Furthermore, each species exhibited a strong fidelity to a single microhabitat type, and the microhabitat preference of each species did not vary over spatial or temporal scales. This is the first record of such a distinct segregation in the microhabitat usage between co-existing rocky shore gastropods in the tropics of the Indo-West Pacific. The consistency of these patterns suggests that biotic factors such as competition for microhabitats may play a greater role in the formation and maintenance of intertidal gastropod aggregations than they were previously thought to.

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A New Species of Abalone (*Haliotis*) from Greece

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Abstract. An undescribed species of *Haliotis* has been discovered in the Aegean and Ionian Seas. It is described herein as *Haliotis mykonosensis*, sp. nov. Although shell morphology of this new species is often similar to the sympatric *Haliotis tuberculata lamellosa* Lamarck, 1822, characteristics of the epipodium and other anatomical features of the soft body parts and analysis of shell measurements show that the two species are clearly distinct. Furthermore, differences in behavior and in the reproductive cycles of these two species have been observed. Epipodial characteristics are also compared with the other Mediterranean taxa *Haliotis stomatiaeformis* Reeve, 1846, and the immigrant *Haliotis pustulata* Reeve, 1846. In addition to epipodial comparisons, shell measurement comparisons have been made with the above three species.

INTRODUCTION

Haliotis tuberculata lamellosa Lamarck, 1822, a variation of *H. tuberculata* Linnaeus, 1758, previously recognized as a subspecies (Geiger, 1998), collected throughout the Mediterranean Sea is known to have highly variable shell characteristics (Ubaldi, 1987). This is also true in the Aegean, Adriatic, and Ionian seas (B. Owen, personal observation). The new species described herein closely resembles *H. t. lamellosa* in shell morphology, and has probably been overlooked in previous collections due to the lack of studies involving the intact animal. The soft parts of *H. mykonosensis* differ most conspicuously in the epipodium, a tentacle-bearing structure, which has a sensory function, and originates from the side of the foot, projecting laterally beyond the edge of the shell (Owen et al., 1971; Cox, 1962). This structure is highly species-specific in its detail and has been used as a primary identifying feature for species (Ino, 1952; Cox, 1962).

Between 1981 and 1997, Owen made a series of trips to study the abalone populations on 11 Greek Islands (Table 1). In 1992, while on the island of Mykonos, Owen observed that some of the abalone had epipodia that were very different from the common *Haliotis tuberculata lamellosa* they were living beside. Epipodial characteristics were also compared with the other Mediterranean taxa *Haliotis stomatiaeformis*¹ Reeve, 1846, and the immigrant *Haliotis pustulata* Reeve, 1846.

MATERIALS AND METHODS

Live abalone were usually found at depths of 1–3 m. Rarely were they found at depths greater than four m. Owen collected a total of 154 *Haliotis mykonosensis* during the same period that he observed or collected approximately 3000 *Haliotis tuberculata lamellosa*. The live specimens were either kept alive in containers of seawater or preserved in 70% isopropyl alcohol. Living material was transported to Gualala, California in 1988, 1991, 1996, and 1997 and maintained by author Owen in several 13 liter aquariums with filtered seawater collected from the local shoreline. A total of 46 *H. mykonosensis* and 45 *H. t. lamellosa* have been studied in aquaria.

Morphological comparisons between the two species involved 154 *Haliotis mykonosensis* and more than 200 *H. t. lamellosa* specimens collected live from the same localities. Radular preparations were examined by scanning electron microscopy. Behavioral contrasts and differences in gonadal development with season were observed in live specimens. Comparisons of epipodia were also made with alcohol-preserved *H. stomatiaeformis* and *H. pustulata*.

Thirty *H. mykonosensis* and 32 *H. t. lamellosa* shells, similarly lacking lamellae formation and comparable in size, were measured for length, width, spire height, and several measurements associated with the suture line (the line formed by the respiratory pores). Data collected on shell measurements are listed in Table 2. Statistical analysis of the above measurements was performed. In the analysis, the size of the shell was normalized by dividing

¹ In a 1998 manuscript on the genera and species of *Haliotis*, Geiger listed a second Mediterranean species *Haliotis neglecta* Philippi, 1848, as both a separate species (Geiger, 1998: table 2) and as a subspecies of *H. tuberculata* (Geiger, 1998: note 5) based only on seven shells. Additional material provided by B. Owen (personal observation) clearly shows the species to be

distinct from *H. tuberculata* and that the correct name for this second Mediterranean species should be *H. stomatiaeformis* (Geiger & Owen, manuscript in progress). The correct name for this species is used herein.

Table 1
Specimen Collection Data

Locale	Years	Number of dive sites	Hours dived (Approx.)	Total <i>H.t. lamellosa</i>	Total <i>H. mykonosensis</i>
Hydra	1981, 1992	3	8	30	0
Mykonos	1981, 1991, 1992, 1996	6	50	150 ^{1,2}	46 ³
Skiathos	1988	3	20	20 ⁴	0
Rhodes	1988	2	11	15 ⁴	0
Paros	1991, 1992	5	25	50 ⁵	5
Santorini	1991, 1996	4	12	12	0
Corfu	1992, 1997	12	25	260 ^{1,6}	94 ⁷
Chios	1992	3	12	30 ⁵	3
Samos	1992	5	12	100 ⁵	6
Naxos	1992	4	10	75 ⁵	0
Crete	1996	4	15	200 ^{8,9}	9
Totals	6	51	> 200	942	154

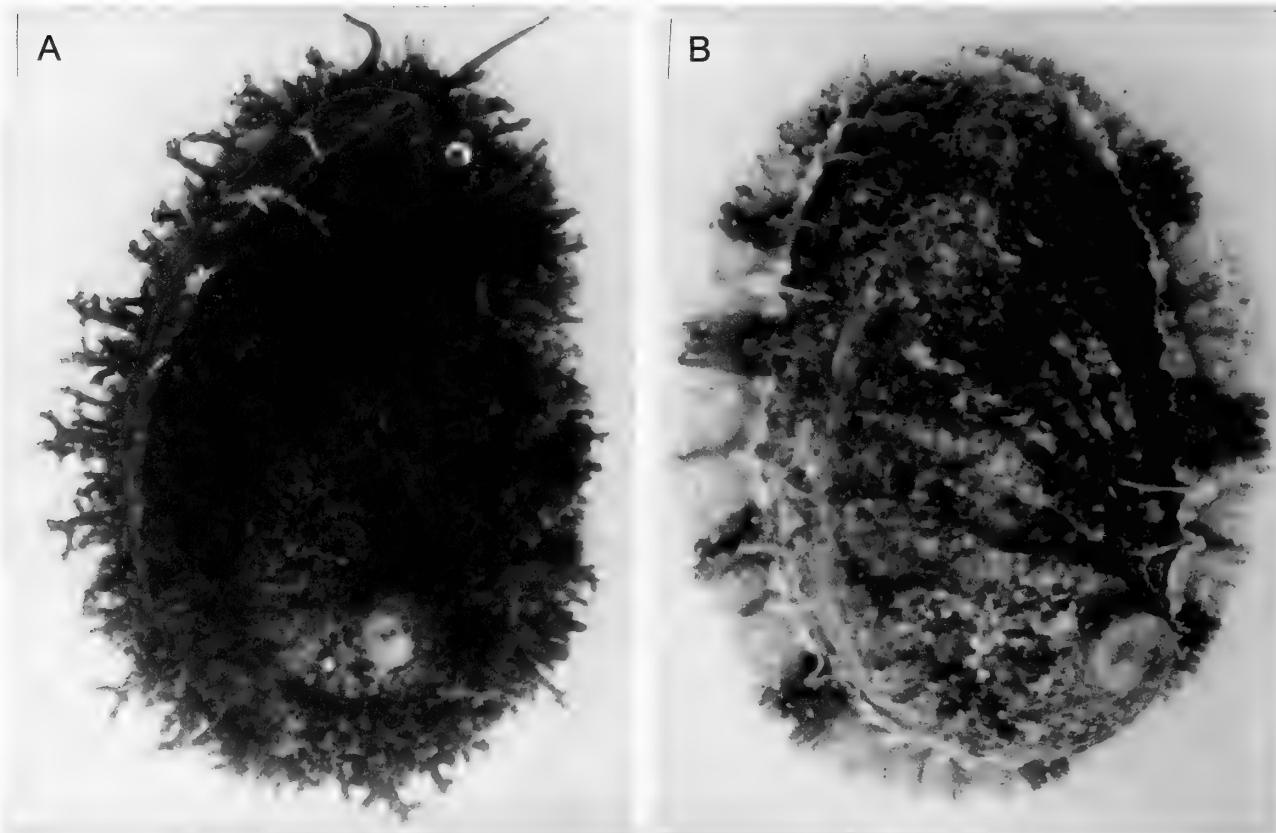
¹ > 500 observed alive but not taken² 37 brought to U.S. alive in 1991³ Seven brought to U.S. alive in 1991 (5) and 1997 (2)⁴ Three brought to U.S. alive (from each island)⁵ > 250 observed alive but not taken⁶ Seven brought to U.S. alive in 1997.⁷ 41 brought to U.S. alive in 1997⁸ > 1000 observed alive but not taken⁹ Two brought to U.S. alive in 1996

Figure 1. Live animals dorsal view. A. *H. mykonosensis* Owen, Hanavan & Hall, sp. nov., 39 mm long. B. *H. t. lamellosa*, 45 mm long. Photographs by B. Owen.

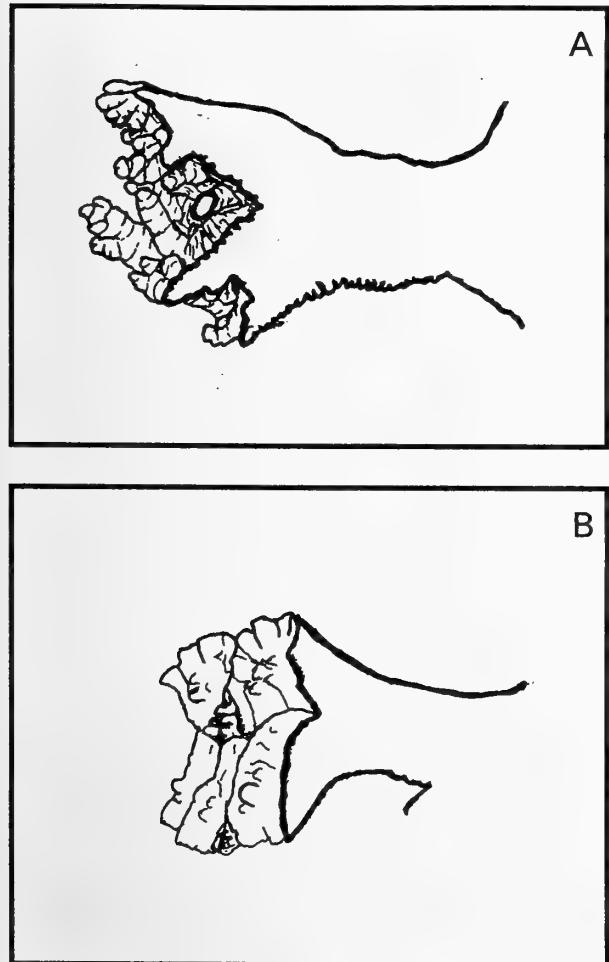


Figure 2. Vertical cross sectional drawing of epipodia of alcohol-preserved specimens. A. *H. mykonosensis* Owen, Hanavan & Hall, sp. nov., $\times 10$. B. *H. t. lamellosa*, $\times 10$.

each shell measurement by the shell's length. A one-way analysis of variance with 95% confidence intervals of the mean based on the pooled standard deviations was used to analyze width and spire placement (the ratio of the distance from the spire to the end of the suture line and the shell length).

The spire inflation was measured by the ratio of the shell's height at $\frac{1}{5}$ the distance from the spire to the end of the suture line and the spire height (R1). The length measurement was not used to normalize this ratio. The distance from suture line to the widest edge of the columella when viewed from the top of the shell was measured and divided by the length (R2). These ratios were graphed against each other and analyzed using a statistical technique called discriminant analysis for multivariate statistics. A detailed discussion of this method can be found in Anderson (1984).

Other Animal Material Examined

Haliotis pustulata. D. L. Geiger collection, date 17 January 1987, Na'Ama Bay, Sinai, Egypt, Gulf of Aquaba; California Academy of Sciences, CASIZ 071896, 5 km SSW of Mora Mora Village, Madagascar, and CASIZ 102287, Tanzania, Zanzibar, north end, Ras Nunswi.

Haliotis tuberculata. D. L. Geiger collection, taken 24 March 1988, Banyuls-sur-mer, southern France, on rock at 0.5 m, brown; D. L. Geiger collection, taken 24 March 1988 Banyuls-sur-mer, southern France, on rock at 0.5 m, green; D. L. Geiger collection, taken 19 August 1989 Isla del Aire, Balearic Islands, Spain; California Academy of Sciences, CASIZ 102314, Ilha Sao Miguel, Azore Islands and CASIZ 099125, Cadiz, Strait of Gibraltar, Isla Tarifa.

Haliotis stomatiaeformis. B. Owen collection, #523 (with animal), Malta; D. L. Geiger Collection, AAB51a, Malta (shell only).

SYSTEMATICS

Family HALIOTIDAE Rafinesque, 1815

Haliotis mykonosensis Owen, Hanavan & Hall, sp. nov.

(Figures 1A, 2A, 3 [left], 4 [left])

Type material: Holotype, California Academy of Sciences, CASIZ 112121. Platy Yialos, Mykonos, Greece, 2 m depth under small flat rock, 19 May 1996, collected by B. Owen. The dimensions of the holotype are: length 38.0 mm, width 23.5 mm, and height 7.8 mm. Paratypes (2), California Academy of Sciences, CASIZ 112122. Platy Yialos, Mykonos, Greece, 2–4 m depth under small flat rock, 19 May 1996, Collected by B. Owen. Paratype #1 measures length 34.5 mm, width 20.0 mm, and height 7.5 mm. Paratype #2 measures length 35.5 mm, width 21.0 mm, and height 7.2 mm.

Etymology: This species is named for the type locality, Mykonos.

Distribution: Thus far found only on five of the 11 islands surveyed. Most common at the more northern Greek islands studied, particularly Corfu. Less common at Mykonos (type locality) and rare at Paros, Chios, and Samos. Thus far found only in areas of *Poisidonea oceanica* (L.) (Riedl, 1983; Larkum et al., 1989), a broad-leaved (~ 1.5 cm wide) green “eel grass.”

Shell morphology: The species exhibits a thin, oblong-ovate, flatly convex shell with between four and seven open respiratory pores. The exterior has fine, smooth spiral cordings, with a shallow post-syphonic groove, infrequently found with lamellae at shell sizes smaller than 25 mm. The exterior shell coloration is variegated olive green, brown, and beige with an occasional totally orange form. The shell exterior often forms a fine radial tenting pattern of the other colors against the beige background.

Table 2
Shell Measurements

Specimen number	Length	Width	Spire to suture line end	Spire height	Shell height ¹	Distance from suture line ²
<i>H. mykonosensis</i>						
90	38	28.5	30.9	7.25	5.8	4.5
37	38.5	23.8	30.4	7.95	5.8	5
13	33.8	19.3	26.45	6.95	5.6	4.2
14	35.5	21.4	28.7	7.05	6.2	4.65
20	38.6	23.1	30.4	9.1	6.9	5.25
8	45.85	28.6	39.5	9	7.7	4.85
34	29.5	18.75	23.7	6.8	5.15	4.5
12	34.8	20.65	26.95	6.7	4.75	4.2
16	35.8	21.95	30	8.2	5.9	4.2
35	28.5	17.5	23.3	6.2	5.05	3.2
24	37	20.4	29.95	7	6	4.5
10	38.5	22.4	29.95	8.4	7.05	5.3
22	31.6	19.15	26.2	6.8	5.1	4.0
7	32.95	19.4	27.6	6.8	5.1	4.2
21	35	19.8	27.35	7.05	6.1	5.3
31	22.7	14.5	18.6	5.1	4.1	3.6
23	38.6	22.35	34.2	9.9	8.2	5.0
18	28.35	17.9	22.8	5.85	4.8	3.4
Unk	30.8	17.55	25.1	6	5.2	4.3
19	29.4	17.25	22.95	6.2	5.3	4.2
36	28.1	27.05	23	6.2	5.25	3.5
15	42.5	26.2	33.85	8.7	7.1	5.8
94	38.35	23.3	31.1	8.9	6.6	4.8
95	40.65	27.3	31.25	9	7.75	4.7
93	36.7	22.5	28.85	8.7	6.95	4.8
16	41.1	24.45	35.1	8.85	6.6	4.5
17	44.4	25.3	36.2	9.5	8.3	ND ³
22	39.8	24.25	31.75	9.4	8.2	ND
7	34.15	21.1	29	7.7	6	ND
19	40.25	24.5	33.45	8.7	8.2	ND
<i>H. tuberculata lamellosa</i>						
1	30.85	18.3	26	7.8	4.3	5.4
2	38.1	23.55	31.5	7.9	5.1	4.8
3	37.95	24.3	30.4	8.8	6.6	5.95
4	34.3	20.75	26.35	7.8	5.7	5.2
5	31.2	29.8	22.4	7.1	5.2	5.2
6	41.8	25.3	33.85	9.2	8.1	6.6
7	32.55	31.8	25.85	6.4	5.1	5.1
8	27.6	17.4	23.4	7.2	5.15	6.05
9	30.85	19.95	25.35	7.6	5.05	4.75
10	35.6	22.1	29.2	7.1	5.2	5.5
11	35.95	21.6	27.3	7.5	4.95	5.0
12	38.6	32.9	31	7.9	5.8	6.0
13	31.1	18.95	25	7.1	5.1	4.6
14	31.7	19.3	25.05	6.8	5.25	4.6
15	31	19.35	25.3	6.7	4.3	4.3
16	33.5	20.8	27.3	8	6.8	4.8
17	31.1	18.3	25.65	7.3	5.9	5.5
18	33.3	19.8	27.4	7.8	6.7	4.6
19	29.4	17.75	24.9	6.9	6.6	5.6
20	27.7	17.3	23.2	6.2	5	4.8
21	30.75	19.4	24.4	7.9	4.75	4.3
22	29.2	17.5	23.25	6.1	3.8	5.6
23	25.1	16.25	20.6	6.15	4.85	4.7

Table 2
(Continued)

Specimen number	Length	Width	Spire to suture line end	Spire height	Shell height ¹	Distance from suture line ²
24	35.2	21.45	28.3	8.3	6.3	5.1
25	29.75	18.15	23.1	6.25	4.6	4.2
26	32.45	20.15	26.75	8.3	5.6	4.7
27	38.6	24.95	33.5	9.2	6.95	6.1
28	41.2	26.35	32.4	11.5	6.7	6.6
29	38.7	24.65	31.5	8.8	6.3	4.8
30	37	21.7	29.8	8.9	6.6	6.3
31	35.4	21.7	29.2	8.4	6.3	5.4
32	33.85	19.4	27.15	8.9	5.9	5.8
<i>H. stomatiaeformis</i>						
1	29.5	27.6	25.85	6.1	6.7	ND
2	24.5	14.55	22.5	6.2	6.05	ND
3	28.5	18	25.75	7.9	7.3	ND
4	26.5	16.05	24.3	6.9	6.9	ND
5	34.5	20.5	30.85	8.2	8	ND
<i>H. pustulata</i>						
1	35.05	22.45	22.5	7.7	5.8	ND
2	38.35	24.75	28.3	8.1	7.2	ND
3	28.4	18.6	21.3	6.2	5.8	ND
4	40.9	25.55	30	8.8	7.3	ND
5	32.85	21.65	23.45	7.2	6.2	ND

¹ Shell height at $\frac{1}{3}$ the distance from spire to the end of the suture line.

² Distance from suture line to the widest edge of the columnella.

³ ND = not done.

Epipodium: The species has a thick epipodial structure with an elongated dorsal margin and smaller ventral margin. The ventral surface is covered with small wartlike papillae and is pigmented. The mid-epipodial region, also pigmented, is covered with large, highly ramified projections, which often subdivide into complex non-symmetrical branching structures. The number and spacing of these large projections vary from one specimen to the next. The basic color of pigmented areas is brown to almost black.

Discussion: When examining the soft body parts of *Haliothis mykonosensis* and *Haliothis tuberculata lamellosa*, anatomical differences between the species are most evident in the epipodium. The side-by-side comparison of live specimens of these two species in Figure 1 clearly shows that the large, highly ramified epipodial projections between the upper and lower epipodial margins of *H. mykonosensis* (Figure 1A) are very different from the small digiform projections of *H. t. lamellosa* (Figure 1B). In *H. mykonosensis*, the projections subdivide into complex non-symmetrical branching structures, which give the living animal a unique appearance. Larger specimens (> 25 mm) have highly developed projections, which can be more than 6 mm in length. *Haliothis tuberculata lamellosa* has small digiform projections, which are simple, blunt, and seldom more than 1 mm. Infrequently, a specimen

will have longer projections (up to 1.5 mm) with a small stellate structure visible at the tip when viewed under a hand magnifier. In addition, the lower epipodial margin of *H. mykonosensis* is not visible from the top view (Figure 1A) in contrast to the clearly visible lower epipodial margin of *H. t. lamellosa* (Figure 1B).

Differences in the epipodium can also be seen in the comparison of alcohol-preserved specimens of *Haliothis mykonosensis* (Figure 2A) and *H. t. lamellosa* (Figure 2B). *Haliothis mykonosensis* has an elongated dorsal margin and the presence of papillae and pigment on the ventral surface. *Haliothis tuberculata lamellosa* has a more elongated ventral margin, clearly visible in Figure 1B, with a smooth unpigmented ventral surface. The pigmented areas of the epipodium of *Haliothis mykonosensis* are brown to almost black, whereas those of *H. t. lamellosa* are grayish green, dispersed in a series of vertical bands.

Comparisons to *Haliothis pustulata* and *Haliothis stomatiaeformis* further support the uniqueness of the epipodial characteristics of *H. mykonosensis*. The epipodium of *H. pustulata* is a thin structure, which has ventral and dorsal margins composed of closely packed fingerlike projections (Geiger, 1996). *Haliothis stomatiaeformis* has an extremely thin epipodium with small digiform structures on the upper and lower margins, and unlike *H. my-*

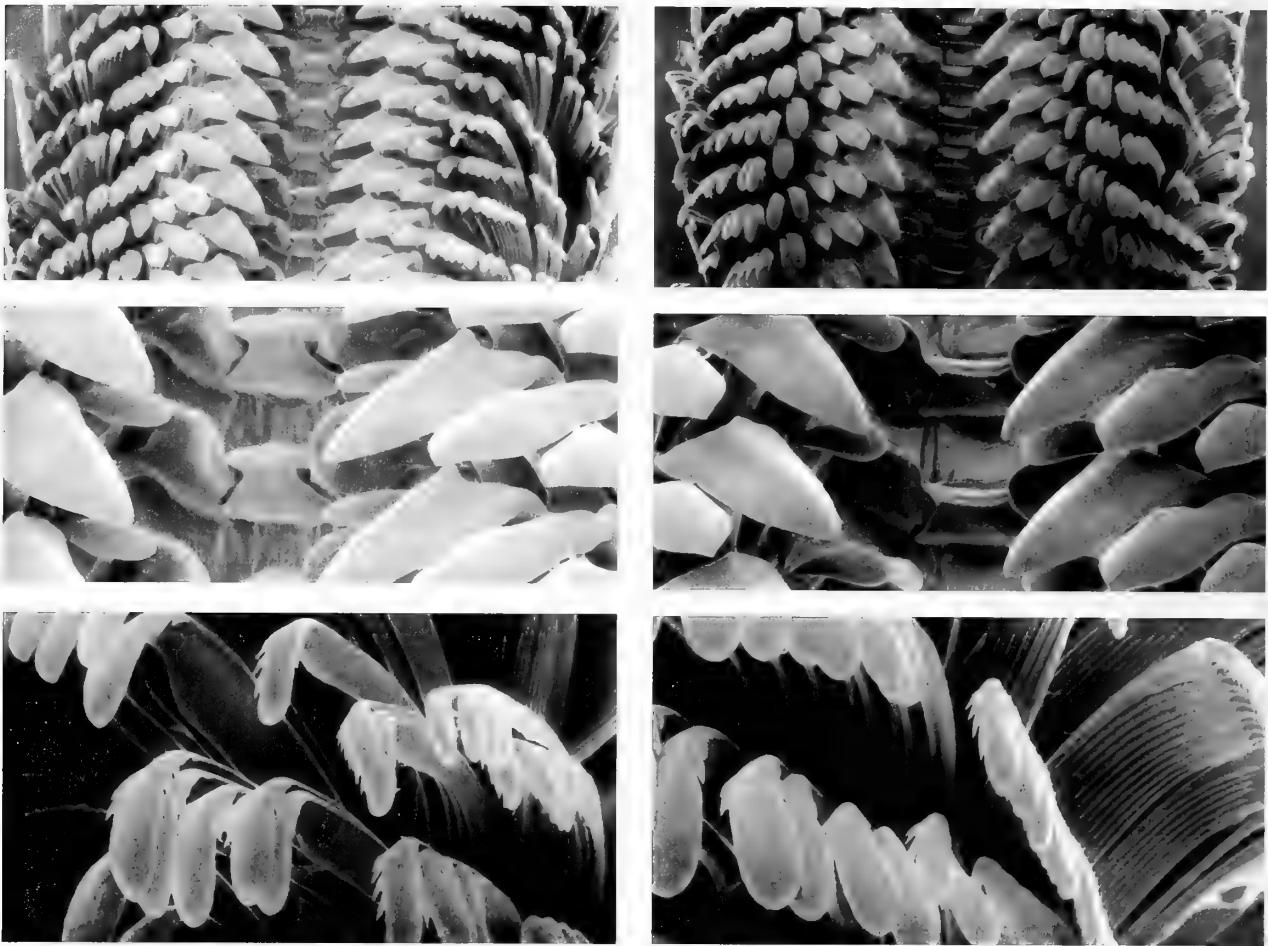


Figure 3. Scanning electron micrographs of radular teeth. Left. *H. mykonosensis* Owen, Hanavan & Hall, sp. nov. Right. *H. t. lamellosa*. Top. Radular teeth $\times 40$. Middle. Rachidian and inner lateral teeth $\times 120$. Bottom. Lateral teeth $\times 200$.

konosensis does not have any large, highly ramified projections between the margins. *Haliotis mykonosensis* has a very thick epipodium with an elongated dorsal margin, which differs from the other species described herein, in which the ventral margin is more elongated than the dorsal margin.

Another notable anatomical difference was observed in the color of the male gonad. The mature male gonad of *Haliotis mykonosensis* is a dull grayish white color. In *Haliotis tuberculata lamellosa* it is a bright pinkish cream color.

Scanning electron micrographs of the radula of *H. mykonosensis* and *H. t. lamellosa* (Figure 3) show the radula of the two species to be similar.

Haliotis mykonosensis resembles *H. t. lamellosa* exclusively in shell morphology. The shell of *H. t. lamellosa* is highly variable with respect to many characteristics of shell sculpture, presence or absence of lamellae, and color patterns (Ubaldi, 1987). To a lesser extent, this is also true of *H. mykonosensis*, which closely resembles *H. t.*

lamellosa in shell size, shape, and number of open respiratory apertures (Figure 4). Both *H. mykonosensis* and *H. t. lamellosa* from Greece possess between four and seven open respiratory apertures, and greater than 90% of the specimens examined have five or six open holes. However, subtle differences in shell sculpture, spire inflation, and color patterns have been observed in a large percentage of shells. *Haliotis tuberculata lamellosa* typically has stronger and wider cording than *H. mykonosensis*, which has fine narrow cording. The spire of *H. t. lamellosa* is typically more inflated than the spire of *H. mykonosensis* as shown in the shell measurements discussed below. The radially placed markings in *H. mykonosensis*, when present, tend to be finer and more consistent throughout growth than in *H. t. lamellosa*.

The most notable difference between the shells of the two species is in the presence of lamellae. *Haliotis tuberculata lamellosa* often has lamellae, and, when present, they can begin to form on the shell starting as small as 3 mm in length. *Haliotis mykonosensis* infrequently devel-

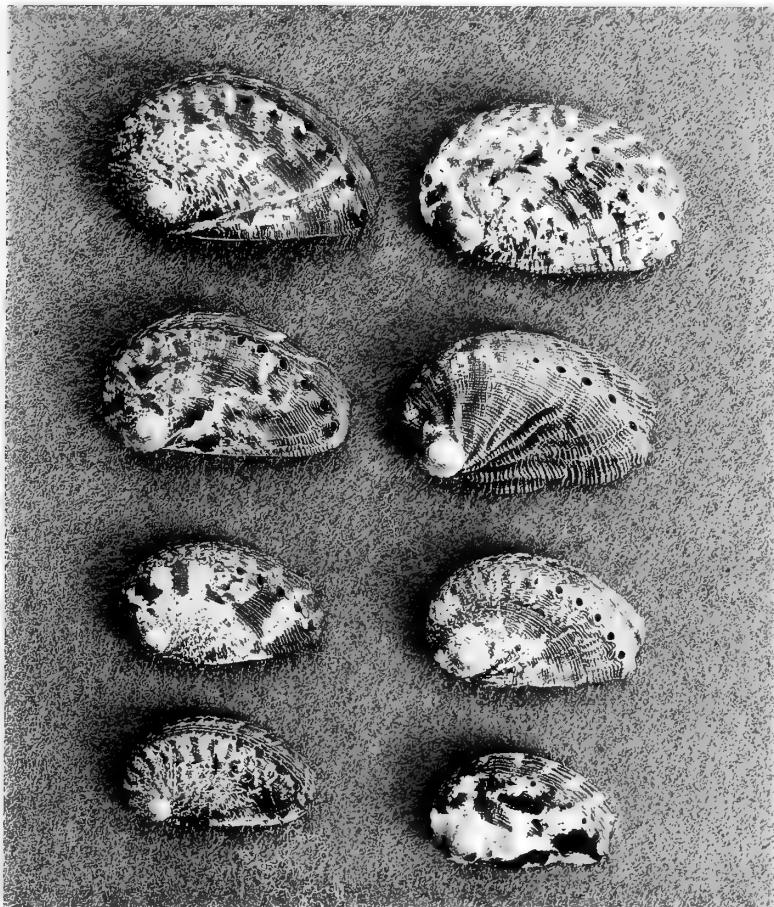


Figure 4. Shell exteriors. Left. *H. mykonosensis* Owen, Hanavan & Hall, sp. nov. (B. Owen collection) Right. *H. t. lamellosa* (B. Owen collection). Length of top left specimen is 44 mm.

ops lamellae. When lamellae are present, they are less pronounced and rarely form at a shell length smaller than 25 mm.

Table 2 presents the shell measurements of *H. mykonosensis*, *H. t. lamellosa*, *H. stomatiaeformis*, and *H. pustulata*. The ratio of the width divided by length showed no significant difference between any of the four species.

Statistical analysis of the measure of spire placement distinguishes *H. mykonosensis* and *H. t. lamellosa* from both *H. stomatiaeformis* and *H. pustulata* with 95% confidence intervals of the mean (Table 3). *Haliothis mykonosensis* does not differ from *H. t. lamellosa* in this comparison.

There are two shell measurements that can distinguish *H. mykonosensis* and *H. t. lamellosa* from one another.

Table 3
Spire placement one-way graphic analysis of variance.

Species	N	Mean	SD*	Individual 95% CIs for Mean Based on pooled SD				
				- - - + - - -	+ - - - + - - -	- - - + - - -	+ - - - + - - -	- - - + - - -
<i>H. pustulata</i>	5	71.545	4.310	(-----*)-----)				
<i>H. stomatiaeformia</i>	5	90.187	1.744					(-----*)-----)
<i>H. mykonosensis</i>	30	81.150	2.804			(-*)		
<i>H. t. lamellosa</i>	32	80.894	2.858			(-*)		
Pooled SD = 2.889				- - - + - - -	+ - - - + - - -	- - - + - - -	+ - - - + - - -	- - - + - - -
				70.0	77.0	84.0	91.0	

* Standard deviation

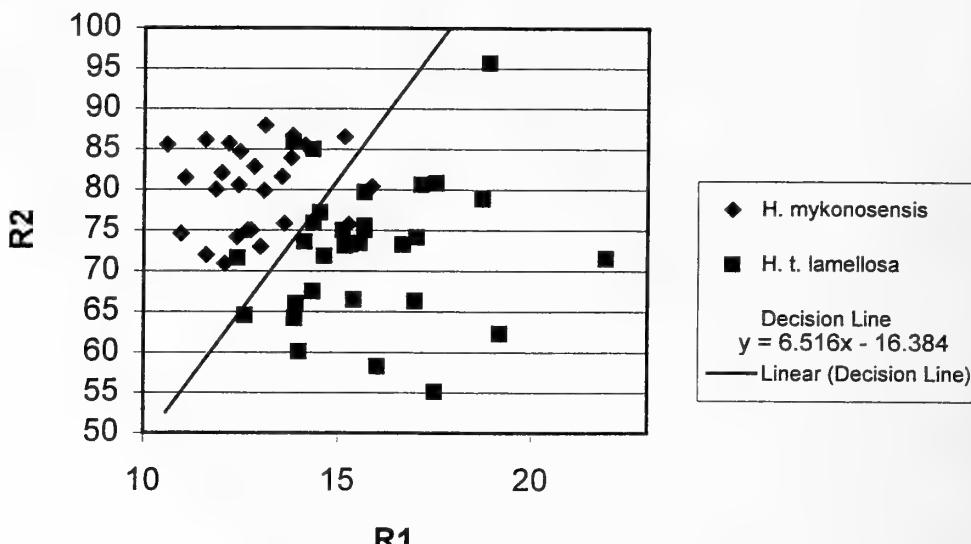


Figure 5. Discriminant analysis of shell measurements. R1 represents the ratio between the shell height at $\frac{1}{5}$ the distance from spire to the end of the suture line and the spire height. R2 represents the ratio of the distance from suture line to the widest edge of the columnella and the shell length. The decision line represents the separation of the two species.

The first is that *H. lamellosa* tends to be more inflated in the spire than *H. mykonosensis* as shown by the ratio of the shell height at $\frac{1}{5}$ the distance from spire to the end of the suture line/spire height (R1). The second difference noted was that the outer edge of the columella extends farther from the suture line in *H. t. lamellosa* than on *H. mykonosensis* as represented by the ratio of the distance from suture line to the widest edge of the columnella divided by the length (R2). When plotted against each other, these two ratios distinguish the two species quantitatively. As can be seen in Figure 5, a graphical presentation of the data along with the decision line, the two species clearly separate according to where these statistics fall on the graph when R1 is plotted on the X axis and R2 is plotted on the Y axis. Statistically, the line optimally separating the two species is $R1 = -16.4 + 6.5 \cdot R2$. This is called the decision line. If $R1 > -16.4 + 6.5 \cdot R2$, then classify the species as *H. mykonosensis*. If $R1 < -16.4 + 6.5 \cdot R2$, then classify the species as *H. t. lamellosa*. Therefore, if the data collected so far are representative of the population as a whole, the correct decision will be made over 90% of the time using this classification scheme alone.

In addition to differences in anatomical and shell features, differences in feeding behavior and locomotion have been observed in aquarium specimens. For 6 years, a group of *H. t. lamellosa* ignored a species of encrusting red algae building up in their aquarium, whereas *H. mykonosensis* actively and preferentially consumed the algae immediately upon introduction into this aquarium. When disturbed into movement by a flashlight at night, there is a substantial difference in speed of locomotion. *Haliothis mykonosensis* almost detaches from the aquari-

um walls, and with a very fluid undulating motion of the foot moves across the aquarium rapidly. Similarly disturbed, *H. t. lamellosa* is less active and moves much more slowly and deliberately. *Haliothis mykonosensis* has also been observed to move rapidly backward when disturbed by a beam of light at night. *Haliothis tuberculata lamellosa* has never been observed to exhibit this behavior, nor has any other species of *Haliothis* studied in aquaria (B. Owen, D. Leighton, personal observation).

A curious observation, which might provide a possible direction for further study, is the difference in seasonal maturity of the male gonad in the two species. In 4 separate years (1981, 1988, 1991, and 1992), *H. t. lamellosa* was observed in the field with very mature gonads, and was actively spawning in October. The mature gonad is easily visible when the animal is removed from the surface to which the animal is attached. The gonad lies alongside the epipodium on the growth side of the shell. None of the *H. mykonosensis* observed had mature gonads in October/November of 1992. Only one specimen of 79 had perceptible evidence of gonad maturation (a male from Samos). *Haliothis mykonosensis* was observed with mature gonads and was actively spawning in May of 1996 and 1997. At the same time, more than 500 adult *H. t. lamellosa* examined had immature gonads and were not observed to spawn, with a single exception of one male from Corfu. This animal spawned minimally (brief expulsion of a trace of sperm) after conditioning in 20–25°C water for 5 days. As these observations included a large number of animals from 11 different islands, in 6 different years, it may suggest that the two species have different reproductive cycles.

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A New Species of the Eulimid Genus *Pelseneeria* Koehler & Vaney, 1908 (Mollusca: Gastropoda) from Staten Island, Argentina

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Abstract. A new species of the eulimid genus *Pelseneeria* is described from Punta Laserre (63°52'49"W, 54°45'06"S), Staten Island, Argentina. *Pelseneeria sudamericana*, sp. nov. lives attached to the test of the echinoid *Pseudechinus magellanicus* (Philippi, 1857). Adults, juveniles, and egg capsules of the new species are illustrated, described, and compared with other living species of the same genus. This is the first report of the genus *Pelseneeria* in South America, and the first record of a eulimid as a parasite of *Pseudechinus magellanicus*.

INTRODUCTION

Few modern papers deal specifically with species of Eulimidae from Argentine waters. Strebler (1908) described *Eulima antarctica* from Burdwood Bank and *Volutaxiella translucens* and *V. subantarctica*, from South Georgia Island. *Volutaxiella subantarctica* was included in the genus *Balcis* Gray, 1847, by Linse (1997) who recorded this species and *Strombiformis carforti* (Rochebrune & Mabille, 1889) from the Beagle Channel, Tierra del Fuego, Argentina. Castellanos (1981) reported *Strombiformis auricinctus* Abbott, 1958, from off Mar del Plata (38°30'S, 57°27'W) in 57 m, *Balcis subcarinata* (d'Orbigny, 1842) from 41°46'08"S, 63°13'05"W in 65 m, and *B. solitaria* (Smith, 1915) from off Bryde Island, Antarctic Peninsula. Later, Castellanos et al. (1987) described several new microgastropods, among them a single eulimid, *Melanella salvadorei* from off Golfo San Jorge, 46°S, 60°W in 600 m depth. Dell (1990) recorded five species of eulimids from Antarctica and pointed out the difficulty of understanding the family without knowing soft parts and host species. *Stilifer polaris* Hedley, 1916, described from the Shackleton Ice Shelf (96°13'E) was included in the genus *Toledonia* Dall, 1902, by Warén (1980) and in *Stilapex* Iredale, 1925, by Dell (1990). In northern South America, Cantera & Neira (1987) recorded the presence of the genus *Echineulima* Lutzen & Nielsen, 1975, from the Colombian Pacific without descriptions of new species. Rios (1994) cited *Stilifer subulatus* Broderip & Sowerby, 1832, and *Pisolamia brychia* (Watson, 1833) as living in Brazilian waters among other species of eulimids.

To date, there have been no reports of the genus *Pel-*

seneeria from South America. The small size and distinctive habitat of this group, as ectoparasites of echinoderms, probably have contributed to the lack of knowledge.

The genus *Pelseneeria* Koehler & Vaney, 1908, groups eulimids that are external parasites on sea urchins (Warén, 1983, Warén et al., 1984; Smith, 1998). Koehler & Vaney (1908) described three species together with the new genus, all from the Azores. Two of these species parasitize the echinoid *Echinus affinis* Mortensen, 1903, and the third lives on *Genocidaris maculata* (Agassiz, 1869). *Pelseneeria hawaiiensis* Warén, Burch & Burch, 1984, from the Hawaiian Islands, lives attached by its proboscis to the echinoid *Aspidodiadema hawaiiensis* Mortensen, 1939. Smith (1998) mentioned *P. brunnea* (Tate, 1889) as a parasite of *Heliocidaris erythrogramma* (Valenciennes, 1846), a common sea urchin in Australia. Powell (1939) created the genus *Venustilifer* to include the species *V. bountyensis* (= *Pelseneeria bountyensis*) which he previously (Powell, 1933) described in the genus *Hypermastus* Pilsbry, 1899. Climo (1971) described the external morphology of *P. bountyensis* and pointed out differences with the genus *Stilifer* Broderip, 1832. In a generic revision of the family Eulimidae, Warén (1983) regarded the following genera as synonyms of *Pelseneeria*: *Parastilifer* Ivanov, 1952; *Turtonia* Rosén, 1910; *Rosenia* Schepman, 1914; and *Venustilifer* Powell. A good account of the genus *Pelseneeria* with remarks on the characters of the whole family is given by Bouchet & Warén (1986) who reviewed the deep water Eulimidae of the northeastern Atlantic.

In this paper a new species of the genus *Pelseneeria* Koehler & Vaney, 1908, the first from Argentine waters, is described.

MATERIALS AND METHODS

Eleven adult shells (most of them severely damaged), and dozens of larval specimens and egg capsules of *Pelseneeria sudamericana*, sp. nov. still attached to two dry specimens of the regular echinoid *Pseudechinus magellanicus* (Philippi, 1857) were found in the mollusk collection of the Museo Argentino de Ciencias Naturales.

Shell ultrastructure data were procured from freshly fractured shell fragments of two broken specimens. The fragments were cut out from the central lip of the last whorl, and examined by SEM. Non-coated material was digitized with a digital scanning camera. All pictures were processed with the software Adobe Photoshop v. 5.02. The material is deposited in the invertebrate collection of the Museo Argentino de Ciencias Naturales "Bernardino Rivadavia," Buenos Aires, Argentina (MACN).

SYSTEMATICS

Family EULIMIDAE H. & A. Adams, 1853

Genus *Pelseneeria* Koehler & Vaney, 1908

***Pelseneeria sudamericana* Pastorino & Zelaya,
sp. nov.**

(Figures 1–12)

Type locality: Punta Lasserre, Staten Island, Argentina ($54^{\circ}45'06''S$, $63^{\circ}52'49''W$); collected in 55 m by the ship A.R.A. *San Luis* in 1933 (Figure 13).

Type material: Holotype (MACN 22028) and two paratypes (MACN 22028-1), all from the type locality (Table 1).

Etymology: From South America because it is the first species of the genus *Pelseneeria* described from this region.

Description: Shell small, suboval, brittle, very thin, bright white in color; protoconch white, blunt, and mucronate, of $2\frac{1}{2}$ whorls; axis in the same angle as that of the adult shell. Teleoconch of $3\frac{1}{2}$ slightly convex whorls; spire less than $\frac{1}{4}$ of total shell length. Suture shallow, slightly impressed; subsutural ramp present, periphery of last whorls angulate. Aperture large, ovate, interior glossy white. Columella thin and smooth, no callus evident in parietal wall. Axial ornamentation of very faint and regular growth lines, slightly inclined.

Operculum and radula lacking. Soft parts very badly preserved. Some specimens still attached by the snout to the test of the host. Snout conical with irregular edges. Shell ultrastructure (Figure 8) of two distinguishable layers, innermost layer (0.75 shell thickness), composed of

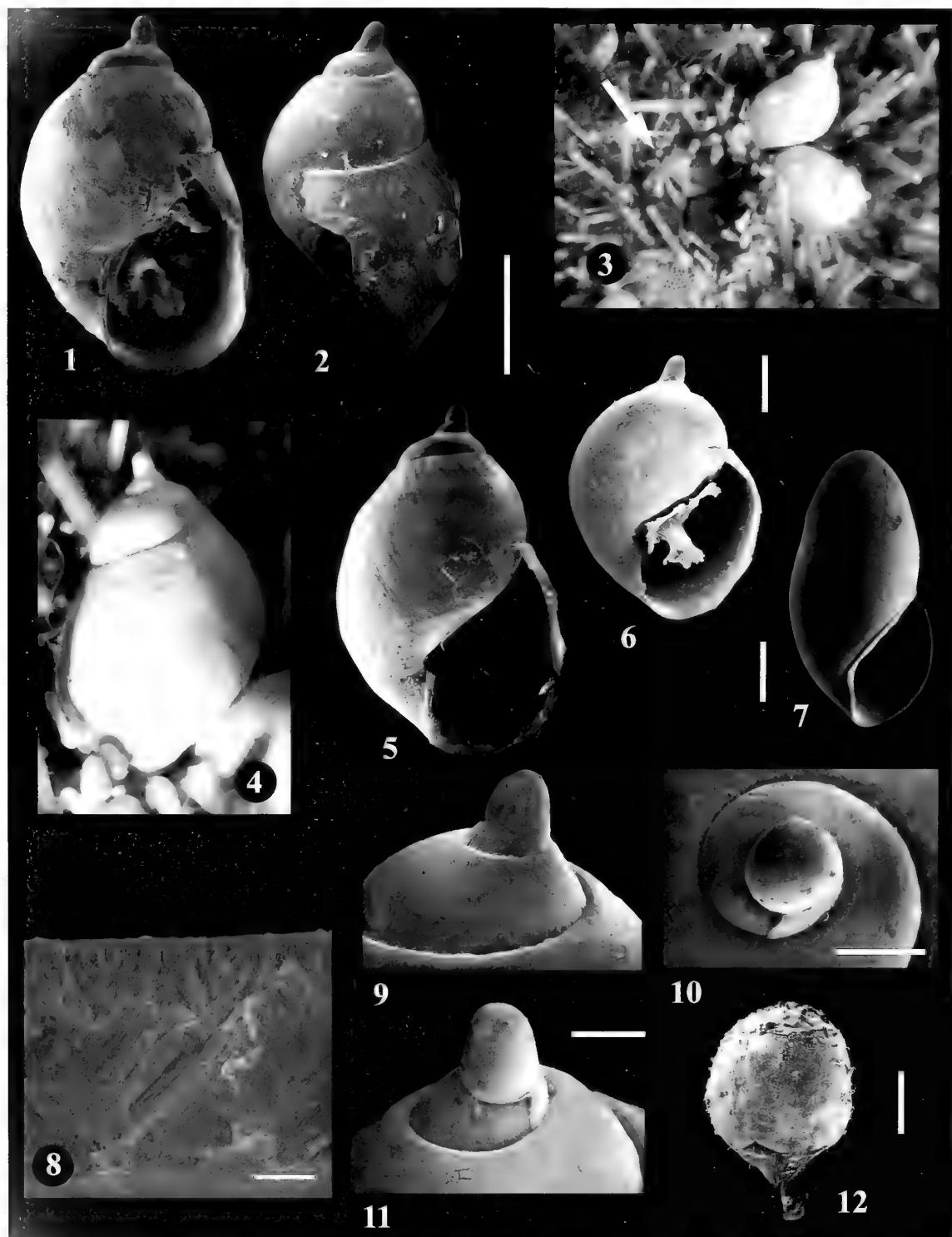
aragonite with the crystal planes oriented parallel to the growing edge; the outer layer of crossed lamellar aragonite with crystal planes oriented perpendicular to growing edge (0.25 shell thickness).

Capsules. More than 50 egg capsules in all stages of development have been found on a single urchin. Capsules are elliptical with irregular edges, attached directly to the test or spines of the urchin by means of a short, thin stalk. Each immature capsule is about $600 \times 700 \mu\text{m}$ in size (Figure 12). Mature capsules are larger and contain several ovoidal embryos each about $440 \mu\text{m}$ in length and $235 \mu\text{m}$ in width (Figure 7).

Remarks: There is no record of any species of *Pelseneeria* from the Magellanic region; however, two species from Australian waters are comparable: *P. bountyensis* (Powell) and *P. brunnea* (Tate). The holotype of *P. bountyensis* was illustrated by Warén (1983:figs. 224, 225), and two paratypes of *P. brunnea* housed at the Australian Museum (#C.006589 from Port Phillip, $38^{\circ}7'S$, $144^{\circ}48'E$) were available for comparison purposes. Both Australian species are more globose than *P. sudamericana*, with their protoconchs heavily covered by the first whorls of the teleoconch. The new species has a subquadrate profile showing a characteristic subsutural ramp that is absent in most of the previously known species. The protoconch is covered only under the middle of the outer lip. The axis of the protoconch of *P. sudamericana* is slightly inclined backward, whereas the protoconchs of *P. bountyensis* and *P. brunnea* are smaller and inclined laterally.

Smith (1998) reported the occurrence of several individuals of *P. brunnea* attached to the center of the aboral surface, each with its long proboscis inserted through a hole in the test of the echinoderm. Three of the largest specimens of *P. sudamericana* were found around the periproct area with the snout attached to the test of the urchin (Figure 3). Two of them had the snout covering the enlarged gonopores, while the third penetrated the test through an elliptical hole. Warén et al. (1984) mentioned *P. hawaiiensis* and *Pelseneeria* sp. (*Stilifer* sp. in Schepman & Nierstrasz, 1909) as the only species of *Pelseneeria* with this particular mode of attachment to the gonopores. As far as we can see on the dry specimens, *P. sudamericana* has the same behavior as well as the ability to penetrate the test. *Hypermastus* Pilsbry, 1899, another eulimid genus that parasitizes irregular echinoids is well known for its ability to drill holes in the test of its host, although details of the drilling process remain unknown (Warén & Crossland, 1991).

Coloration of most of the *Pelseneeria* species is translucent yellowish or brown (Bouchet & Warén, 1986; Warén, 1983). Adult dry specimens of *P. sudamericana* still attached to the echinoid test are opaque white, although one juvenile had a translucent shell. The protoconch is always white.



Figures 1–12. *Pelseneeria sudamericana* Pastorino & Zelaya, sp. nov. Figures 1, 2. Holotype MACN 22028. Figure 3. Holotype (down) and paratype (up) in life position, arrow: head the anal area of the sea urchin. Figures 4, 5. MACN 22028-1. Scale bar for figures 1, 2, 4, 5 = 1 mm. Figure 6. Paratype MACN 22028-1, juvenile specimen, scale bar = 400 μ m. Figure 7. Larval specimen free living on the urchin surface, scale bar = 100 μ m. Figure 8. Ultrastructure of the shell, scale bar = 5 μ m. Figures 9–11. Protoconch, three different views, scale bar = 200 μ m. Figure 12. Dry immature egg capsule attached to the test of the urchin, scale bar = 250 μ m.

Table 1

Measurements of the type specimens of *Pelseneeria sudamericana*, sp.nov. in mm.

Specimens	Total Length	Total Width	# Whorls	MACN #
Holotype	2.93	1.87	3½	22028
Paratype 1	2.87	1.91	3½	22028-1
Paratype 2	2.137	1.47	2½	22028-1

The host: *Pseudechinus magellanicus* (Philippi, 1857), a very common species ranging from 35°S, off Rio de la Plata, Argentina, through the Magellan Strait and throughout Tierra del Fuego, to Puerto Montt, Chile. The depth range is also very large, from intertidal pools, to 340 m. According to Bernasconi (1953), this is the most common species of sea urchin in South America. Amazingly, only two specimens among several hundred examined were found to be parasitized by *Pelseneeria sudamericana*. It is not known if some special condition for the development of the parasite exists at the type locality.

Apparently there is no obvious host specificity for species of the genus *Pelseneeria* around the world (see Table 2). *Pelseneeria hawaiiensis* parasitizes echinoids of the genus *Aspidodiadema* Agassiz, 1879, which belongs to a different order than *Helicocidaris* Agassiz & Desor, 1846, which is the host of the Australian *P. brunnea* (Tate, 1889). However, *P. sudamericana* parasitizes the only

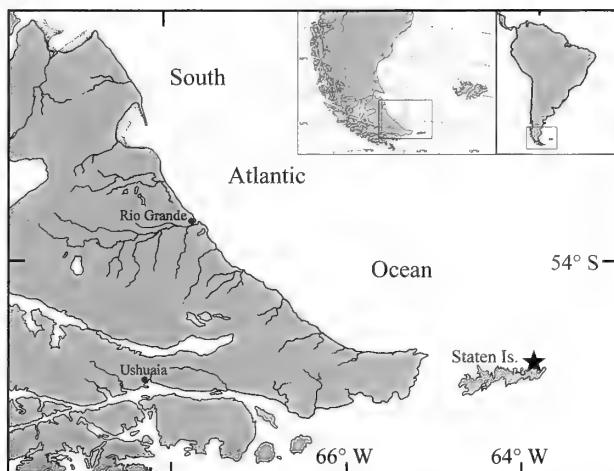


Figure 13. Map showing the type locality (★) of *Pelseneeria sudamericana* Pastorino & Zelaya, sp. nov.

species of *Pseudechinus* Mortensen, 1903, in the southwestern Atlantic, and, *P. bountyensis* from New Zealand lives on another species of the same genus. In general, the hosts belong to different taxonomic groups of sea urchins. As far as we know, no *Pelseneeria* species were recorded as parasites of irregular sea urchins.

Agassiz & Clark (1908) pointed out the presence of more numerous spines on the genital plates of *Aspidodiadema hawaiiensis* Mortensen, 1939, where the parasites (*Pelseneeria hawaiiensis* Warén, Burch & Burch, 1984)

Table 2

Species of *Pelseneeria*, with their hosts and collection depths when known.

<i>Pelseneeria</i> spp.	Hosts and Depth	Source
<i>P. sudamericana</i> , sp. nov.	<i>Pseudechinus magellanicus</i> , 55 m	This paper
<i>Pelseneeria</i> sp.	<i>Caenopedia cubensis</i> , 541 m	Bingham & Young, 1993
<i>Pelseneeria</i> sp. (as <i>Stilifer</i> sp.)	<i>Aspidodiadema tonsum</i> , ?	Schepman & Nierstrasz, 1909, Warén et al., 1984
<i>Pelseneeria</i> sp.	<i>Stereocidaris hawaiiensis</i> , 520 m	Warén et al., 1984
<i>P. bountyensis</i> (Powell, 1933)	<i>Pseudechinus novaezealandiae</i> , 311–840 m	Powell, 1979, Climo, 1971
<i>P. brunnea</i> (Tate, 1889)	<i>Helicocidaris erythrogramma</i> , ?	Smith, 1998
<i>P. castanea</i> (Dall, 1925)	<i>Strongylocentrotus nudus</i> , <i>S. intermedius</i> , 15–18 m	Musashi & Habe, 1991, Habe, 1992
<i>P. hawaiiensis</i> Warén, Burch & Burch, 1984	<i>Aspidodiadema hawaiiensis</i> , 470–580 m	Warén et al., 1984
<i>P. media</i> Koehler & Vaney, 1908	<i>Echinus affinis</i> , 1085–1919 m	Koehler & Vaney, 1908, Bouchet & Warén, 1986
<i>P. minor</i> Koehler & Vaney, 1908	<i>Genocidaris maculata</i> , 67–185 m	Koehler & Vaney, 1908
<i>P. minuta</i> (Dall, 1927)	?, 678 m	Dall, 1927, Bouchet & Warén, 1986
<i>P. profunda</i> Koehler & Vaney, 1908	<i>Echinus affinis</i> , 1940 m	Koehler & Vaney, 1908
<i>P. sibogae</i> (Schepman, 1909)	<i>Temnotrema maculatum</i> , <i>Salmacis dussumieri</i> , <i>Prionechinus sagittiger</i> , 32–835 m	Schepman, 1909, Warén, 1983
<i>P. striata</i> Bouchet & Warén, 1986	<i>Trigonocidaris albida</i> , 275 m	Bouchet & Warén, 1986
<i>P. stylifera</i> (Turton, 1825)	<i>Strongylocentrotus</i> , <i>Echinus esculentus</i> , <i>E. elegans</i> , <i>Psammechinus miliaris</i> , 0–800 m	Lebour, 1932 (as <i>Stilifer stylifer</i>)
<i>P. thurstoni</i> (Winckworth, 1936)	?, 18 m	Winckworth, 1936, Warén, 1983

were attached. Warén et al. (1984) suggested that despite the low number of observations (two specimens) these spines could be an adaptive protection from fishes. We cannot distinguish differences in the spines of the genital plates from parasitized and non-parasitized sea urchins.

Most of the species of *Pelseneeria* live at bathyal depths (see Table 2). However, *P. sudamericana* was found in 55 m. The whole collection of echinoderms of the Museums of La Plata (MLP) and Argentino "Bernardino Rivadavia" (MACN) was searched. Among 600 specimens of *Pseudechinus magellanicus* and other species of urchins of different genera, only two specimens from the same lot of six were found to harbor the ectoparasites. This fact leads us to suggest that this species either normally has a deeper bathymetric range and only rarely occurs in shallow waters, or it is very uncommon.

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A New Species of the Land Gastropod Genus *Solaropsis* Beck, 1837 (*Helicoidea*: *Camaenidae*) from Bolivia

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Abstract. A new species from Bolivia of the neotropical genus *Solaropsis* is described and illustrated using morphological characters from the shell, reproductive, pallial, nervous, and digestive systems. The new species is compared in detail with species of the genus with known anatomy. *Solaropsis chicomendesi*, sp.nov. is distinguished on the basis of its shell aperture, sculpture, and anatomical characters, mainly those of the penial complex in the reproductive system.

INTRODUCTION

Solaropsis Beck, 1837, is a neotropical genus of land snail that typically inhabits forests. It lives on trees or under fallen tree branches on the ground and is distributed from Costa Rica to northeastern Argentina. *Solaropsis* was created by Beck (1837) and later assigned to the Camaenidae. Wurtz (1955) reviewed the anatomy of the American Camaenidae excluding *Solaropsis* from the Camaenidae. Later, Nordsieck (1986) gave familial status to *Solaropsis*, establishing the Solaropsidae. For the reasons we discuss below (see Discussion) we retain *Solaropsis* in Camaenidae and reject the taxon Solaropsidae Nordsieck.

The general knowledge of the genus is scanty, and although 44 nominal species were catalogued under this genus (Richardson, 1985), very little is known concerning its anatomy and habits. The main studies on systematics and anatomy were carried out by Von Ihering (1900, 1912); Pilsbry (1890, 1957); Weyrauch (1956); Haas (1956); Tillier (1980, 1989), among others.

The aim of this study is to describe a new species of *Solaropsis* from Bolivia, comparing the anatomy of this species with that of other species of the genus whose anatomy is known.

MATERIALS AND METHODS

Adult specimens were collected from Bolivia, Santa Cruz Department, Angel Sandoval Province, Santo Corazón ($17^{\circ}58'24"S$, $58^{\circ}48'28"W$), during summer (November 1997).

The specimens were drowned in water and fixed in 96% ethanol and later transferred into 70% ethanol. Dissections were carried out under a Leica MZ6 dissection microscope, and illustrations were made with the aid of a camera lucida. Shell measurements were taken with the aid of a caliper (see Table 1). Major diameter of the shell was taken including the width of the outer lip of the peri-

stome. Minor diameter is a measurement of the shell perpendicular to the major diameter. Radula and jaw were prepared for scanning electron microscopy according to Ploeger & Breure (1977). Micrographs were obtained using a JEOL Scanning Electron Microscope 35CF. Terminology used for the descriptions of the reproductive system follows Tompa (1984); pallial, digestive and nervous systems follow Tillier (1989).

RESULTS

Class GASTROPODA

Subclass PULMONATA

Order STYLOMMAТОPHORA

Superfamily HELICOIDEA

Family CAMAENIDAE Pilsbry, 1895

Genus *Solaropsis* Beck, 1837

Type species: *Solaropsis undata* (Lightfoot, 1786) = *S. pellisserpentis* (Chemnitz, 1795) = *S. cicatricata* (Beck, 1837).

Solaropsis chicomendesi Cuezzo & Fernández,
sp.nov.

(Figures 1–4)

Type locality: Bolivia, Santa Cruz Department, Angel Sandoval Province, Santo Corazón, $17^{\circ}58'24"S$, $58^{\circ}48'28"W$.

Type material: Holotype is deposited in the malacological collection of Museo de Historia Natural “Noel Kempff Mercado,” Santa Cruz de la Sierra, Bolivia.

Additional paratypes (four adults) are deposited in the malacological collection of Fundación Miguel Lillo, Universidad Nacional de Tucumán, San Miguel de Tucumán, Argentina. Collection number: FML 14174.

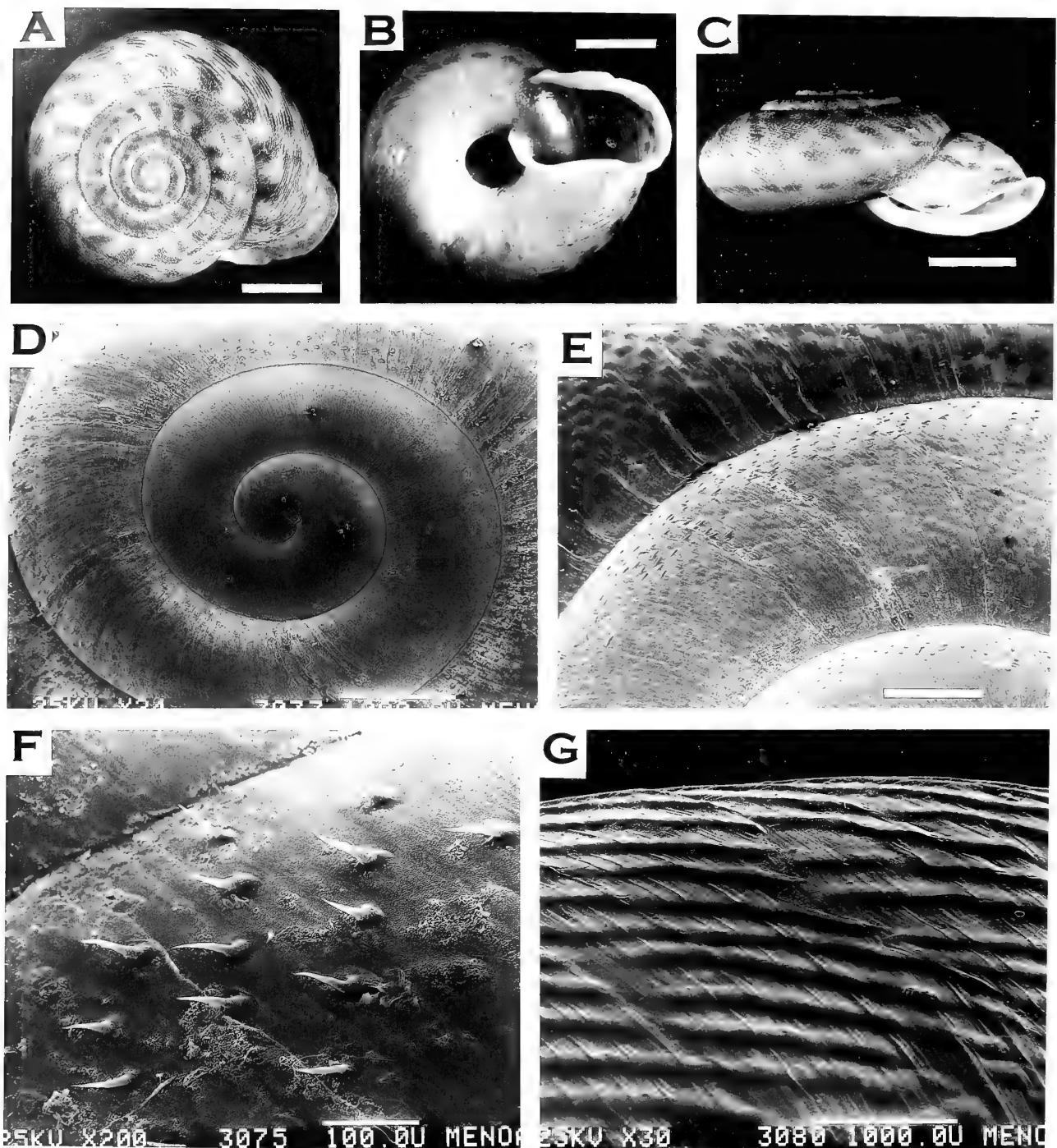


Figure 1. *Solaropsis chicomendesi* Cuezzo & Fernández, sp. nov. Shell Holotype. A. Dorsal view, scale bar = 5 mm. B. Ventral view, scale bar = 5.5 mm. C. Lateral view, scale bar = 5 mm. D. Detail of the protoconch. E. Detail of the third whorl, note the position of hairs and the granules, scale bar = 1000 μ m. F. Detail of the hairs, scale bar = 100 μ m. G. Oblique ribs in body whorl, scale bar = 1000 μ m.

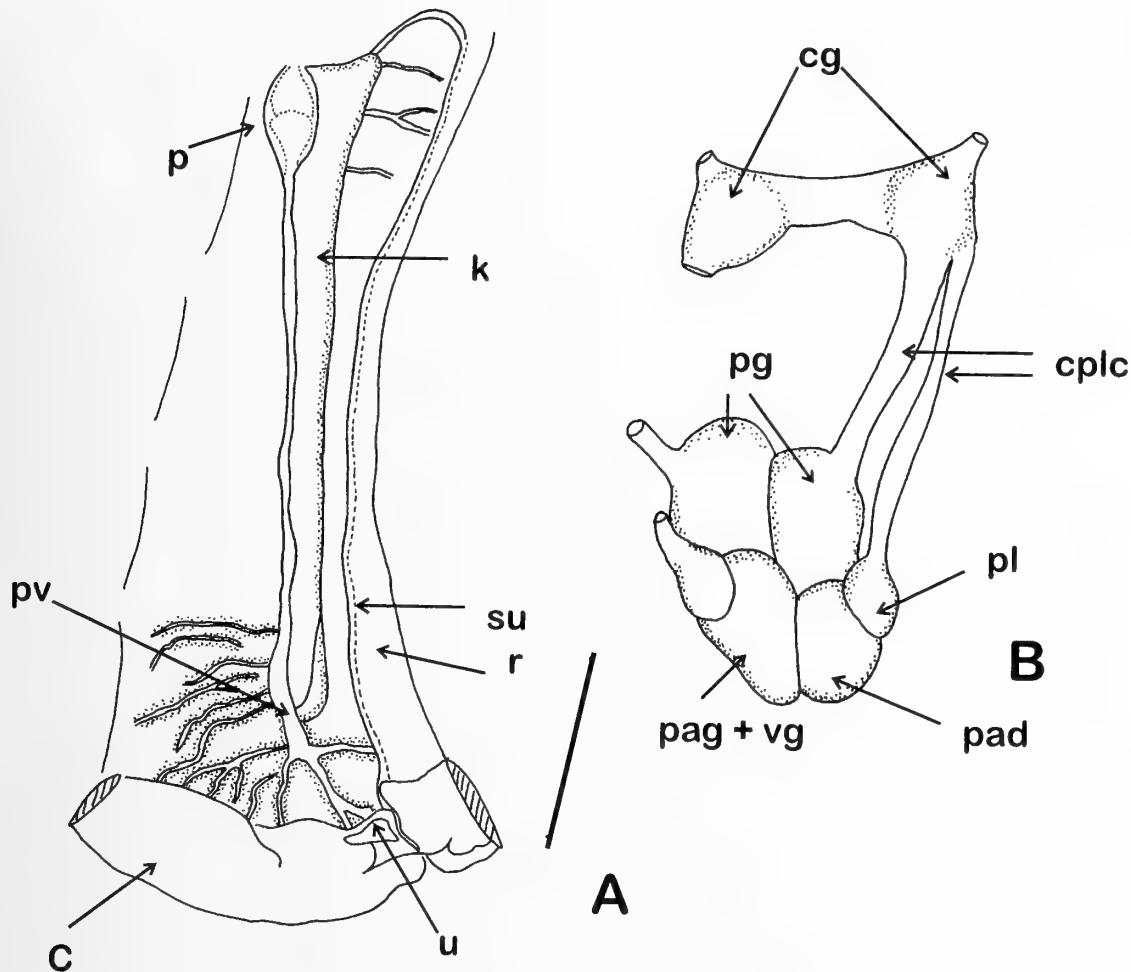


Figure 2. *Solaropsis chicomendesi* Cuezzo & Fernández, sp. nov. (Paratype FML 14174). A. Pallial system, scale bar = 5 mm. B. Central nervous system, dorsal view. Abbreviations: c, mantle collar; eg, cerebral ganglia; cplc, cerebro-pleural connectives; k, kidney; p, pericardium; pad, right parietal ganglion; pag, left parietal ganglion; pg, pedal ganglia; pl, pleural ganglia; pv, pulmonary vein; r, rectum; su, secondary ureter; u, ureteric interramus; vg, visceral ganglion.

Diagnosis: Recognized by its small and fragile shell with the last whorl descending abruptly behind the aperture. Aperture ventral, subquadangular, lips narrowly expanded. Superior lip slightly undulated. Free oviduct inserting at an angle in the vagina which is continuous with bursa copulatrix duct. Flagellum short and thick, penis with an internal pilaster for its entire length. Epiphallus reflected over penis.

External morphology of the body: Animal brownish, with two broad, dark pigmented bands that run parallel to each other from the mantle collar to the ocular tentacles; mid-dorsal groove well marked; basal sole not divided; genital orifice ogival in shape, located below right ocular tentacle.

Shell (Figure 1, Table 1): Shell dextral, helicoid, small, with spire depressed, thin, translucent, fragile; with 4½ convex whorls, not angulated, last whorl descending

abruptly near the aperture; sutures moderately deep, hirsute, with short hairs scattered above and below sutures; umbilicus retrospective, partially overlapped by the peristome; aperture ventral, oblique, subquadangular, peristome fragile, narrowly reflected all around, with superior lip slightly undulated; upper whorls, except the nepionic, densely granulose and on the body whorl the granules arranged in oblique ridges particularly marked behind aperture; chestnut-colored dorsally with a sutural and sub-sutural interrupted peripheral band alternating with angulated perpendicular thicker spots; below the periphery light yellowish-chestnut. Shell measurements of the holotype and paratypes in Table 1.

Pallial complex (Figure 2A): Pallial complex composed of lung, kidney, and heart; lung roof mottled with black spots especially dense close to the mantle collar; proximal extreme of lung roof extending beyond top of kidney

Table 1

Shell measurements of holotype and paratypes of *Solaropsis chicomendesi*, sp.nov. PT = paratypes.

Shell Measurements (mm)	Holo-type	PT#1	PT#2	PT#3	PT#4	\bar{x}
Major diameter	21	20.7	21.3	20.5	19.9	20.68
Minor diameter	17.5	17.9	18.2	18	17.7	17.86
Apertural width	11.5	11.6	11.3	11.4	10	11.16
Total height	8.3	8.0	9.4	8.5	8.1	8.46

(about 2 mm), distal portion limiting with the mantle collar; kidney long and thin running parallel to secondary ureter and extending 90% of the pulmonary roof length, internally with longitudinal thin lamellae, thicker in the proximal portion of the organ; pericardium located in upper left side of kidney; main pulmonary vein runs parallel to left side of kidney and splits into three main branches before reaching mantle collar, many other minor veins running transversely to main pulmonary vein; lung floor or diaphragm membranous, translucent, and thin; secondary ureter runs parallel to rectum and closed in all its extension until reaching mantle collar; ureteric interramus triangular in shape and deeply excavated.

Reproductive system (Figure 3): Hermaphroditic gonad (ovotestis) (Figure 3C) consisting of multiple round acini bearing dark points of pigmentation, embedded in digestive gland, thin ducts of acini converging into hermaphroditic duct, which runs along columellar side; initial portion of hermaphroditic duct slender, central portion swollen, in zigzag, forming vesicula seminalis; fertilization pouch-spermathecal complex (FPSC) not evident outside albumen gland, last portion of hermaphroditic duct inserting directly into distal portion of albumen gland, this organ pale yellow and bean-shaped, continuous with spermoviduct, a long and convoluted tubular organ (Figure 3A); female portion (uterine portion containing seminal groove) of spermoviduct transversely sacculated; distally, spermoviduct splitting into free oviduct and vas deferens; free oviduct with internal thin longitudinal folds for its entire length; vas deferens, a long thin duct, running to distal portion of genitalia where it turns toward proximal portion of penial complex, inserting in proximal region of epiphallus; duct of bursa copulatrix continuous with vagina with free oviduct inserted in an angle with vagina; bursa copulatrix duct wide in its distal portion, sac swollen and elongated; a thin blind diverticulum arising at angle formed by free oviduct and bursa copulatrix duct (Figure 3B); diverticulum running parallel to bursa, attached by tissue to it, and reaching middle zone of spermoviduct with its blind extremity, internally, distal portion of bursa copulatrix duct with same sculpture as proximal portion of vagina, consisting of thin parallel folds;

vagina short ($\frac{1}{4}$ of penis length) ending in genital atrium at same level as penis; penial complex composed of flagellum, epiphallus, and penis; flagellum thick, cylindrical, and short, internally a thick pilaster continuous with proximal portion of epiphallus; epiphallus about three times as long as flagellum with same diameter, reflected over proximal portion of penis and attached to penis sheath by tissue; penis thicker in diameter, about three times as long as epiphallus, internally with a thick pilaster composed of lamellae in zigzag pattern; rest of the penis sculpture consisting of thin, undulating transverse ridges; distal portion of penis with thin longitudinal folds; penis sheath muscular, overlapping entire penis length (Figures 3D, E); atrium with same internal sculpture as distal portion of penis.

Digestive system (Figure 4): The arrangement of the digestive tract follows the general patterns described for Stylommatophora (Tillier, 1989). Jaw arcuate, with 12 thin parallel ribs well marked (Figure 4A), transverse fine striae present on its entire surface, especially marked between ribs, less marked perpendicular lines giving a reticulate impression on the rib surface and marginal plates (Figure 4B); radula thin and long ($33 + 1 + 33 \times 120$); central tooth with tricuspid crown, high mesocone, two times longer than ectocones, laterals bicuspid with high mesocone (Figures 4C, D), marginals tricuspid to multicuspид with ectocones and an endocone, mesocone progressively reduced to the margins of the radula (Figures 4E, F), basal plate of marginal teeth compared to central tooth reduced in length but not in width; buccal mass muscular, round to ovoid; esophagus opening dorsally from buccal mass and progressively increasing in size, forming an esophageal crop, its wall presenting longitudinal thin, deep ridges; two long salivary glands appressed to esophagus, with their main ducts opening into buccal cavity on each side of the esophageal opening; distal portion of glandular bodies joining together over esophageal crop; gastric crop cylindrical; stomach receiving posterior and anterior ducts of digestive gland; two internal typhlosoles arising from point of insertion of ducts of digestive gland, typhlosoles running into proximal intestine, the one beginning at opening of anterior duct longer; intestine running along columellar side of visceral mass turning down under anterior portion of gastric crop and then forming periaortic intestinal loop; rectum following intestine running parallel to pulmonary roof and ending at mantle collar.

Central nervous system (Figure 2B): Entirely contained in pedal cavity, composed of two dorsal ganglia and a ventral chain; both dorsal ganglia connected by a short cerebral commissure and located above esophagus; cerebropleural connectives running obliquely backward connecting dorsal ganglia to ventral chain, forming a ring around esophagus; ventral chain composed of right and left parietals and a visceral ganglion; visceral ganglion

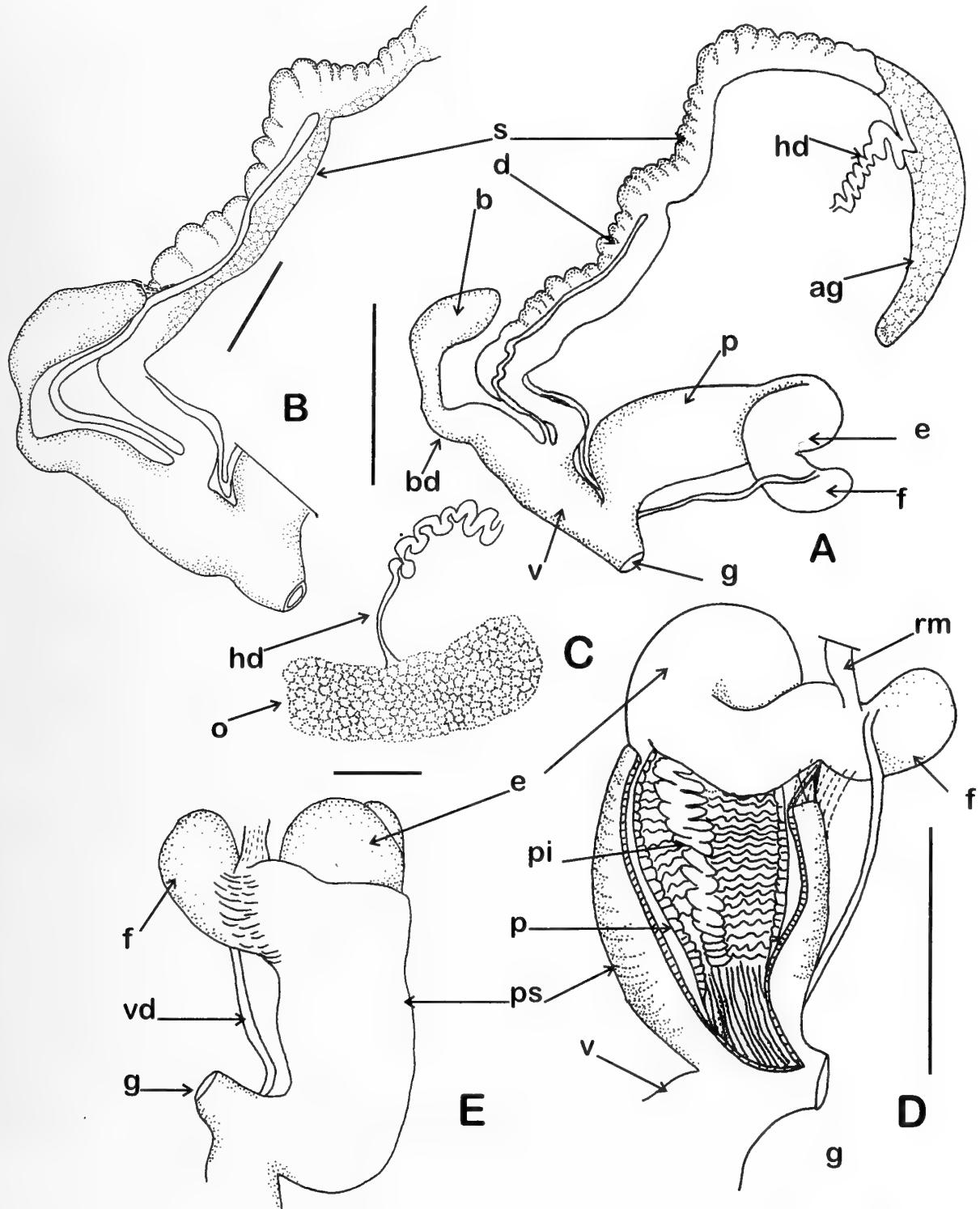


Figure 3. *S. chicomendesi* Cuezzo & Fernández, sp. nov. (Paratype FML 14174). A. Dorsal view of the reproductive system, scale bar = 5 mm. B. Detail of female terminal genitalia, scale bar = 2 mm. C. Ovotestis, scale bar = 2 mm. D. Penial complex with penis wall and sheath longitudinally cut, scale bar = 5 mm. E. Penial complex in ventral view. Abbreviations: ag, albumen gland; b, bursa copulatrix; bd, bursa copulatrix duct; d, diverticulum; e, epiphallus; f, flagellum; g, genital orifice; hd, hermaphroditic duct; o, ovotestis; p, penis; pi, pilaster; ps, penial sheath; rm, penial retractor muscle; s, spermoviduct; v, vagina; vd, vas deferens.

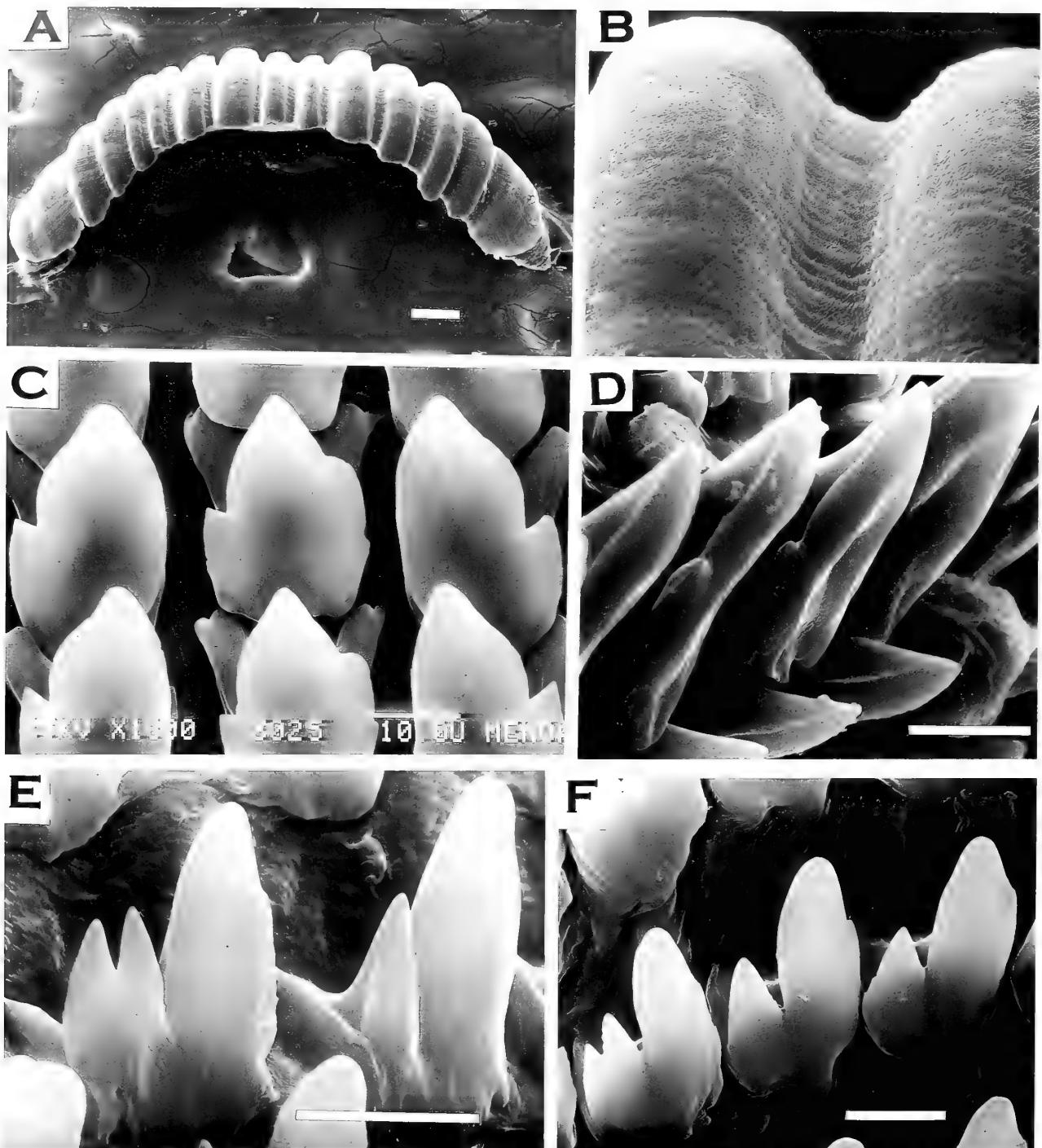


Figure 4. *S. chicomendesi* Cuezzo & Fernández, sp. nov. (Paratype FML 14174). A. Jaw, scale bar = 100 µm. B. Detail of the sculpture of dorsal surface, scale bar = 10 µm. C. Radula: central and first lateral teeth in dorsal view, scale bar = 10 µm. D. Detail of central tooth and lateral teeth, scale bar = 10 µm. E. Transition from lateral #23 to first marginal teeth, scale bar = 10 µm. F. Marginal teeth in erected position, scale bar = 10 µm.

Table 2

Comparative characters between *S. chicomendesi* and the other species of the genus with known anatomy.

Characters	<i>Solaropsis chicomendesi</i> , sp.nov.	<i>Solaropsis heliaca</i> (d'Orbigny, 1835)	<i>Solaropsis brasiliiana</i> (Deshayes, 1832)	<i>Solaropsis angulifera</i> Haas, 1955	<i>Solaropsis undata</i> (Lightfoot, 1786)	<i>Solaropsis marmatensis</i> (Pfeiffer, 1854)	<i>Solaropsis nubeculata</i> (Deshayes, 1831)	<i>Solaropsis gibboni</i> (Pfeiffer, 1846)
Shell	Convex, thin, fragile, whorls	Subcarinate, thin, 5–6 whorls	Convex, solid, 5 whorls	Convex, 4½ whorls	Convex, solid, 6 whorls	Convex, fragile, 4–4½ whorls	Convex, 4½–5 whorls	Carinated, solid.
Shell size (in mm)	Diam. maj: 20–21 Diam. min: 17–18 Alt.: 8–9	Diam. maj: 29–37 Diam. min: 12–16 Alt.: 17–19	Diam. maj: 33–42 Diam. min: 27–34 Alt.: 17–19	Diam. Maj: 29.6 Diam. min: 25 Alt: 14.7	Diam. maj: 40–48 Diam. min: 35–40 Alt.: 22–25	Diam. maj: 11–12 Diam. min: 9–10 Alt: 6	Diam. maj: 18.4 Diam. min: 11–12 Alt.: 27–28	Diam. maj: 60–63 Diam. min: 51–54 Alt.: 27–28
Shell sculpture	Granules and zigzag ridges	Granules and zigzag ridges	Regularly granulate, granules arranged into oblique rows	Regularly granulate, scattered peripheral hairs	Wavy, undulated rugae, granulated	Minutely granulate	Granulated	Coarsely striate, not granulated
Shell aperture	Ventral, subquadrate, peristome thin, slightly reflexed	Oblique, broader than high, peristome wide, reflexed	Oblong-lunar, slightly oblique, peristome narrowly expanded	Semilunar with slightly expanded peristome	Broad-lunar, little oblique, peristome white, reflexed all around	Rounded-lunar, peristome thin, slightly expanded	Semilunar, wider than high, peristome thin, slightly expanded	Broad-lunar, oblique, peristome reflexed all around
Shell spire	Moderately elevated	Moderately elevated	Depressed, apex obtuse	Depressed, apex nearly flat, apex obtuse	Elevated	Near flat	Moderately elevated	Elevated, obtuse
Kidney length	90% of pulmonary roof length	90% of pulmonary roof length	70–80% of pulmonary roof length	70–80% of pulmonary roof	Half the length of the pulmonary roof	80–90% of pulmonary roof length	80–90% of pulmonary roof length	25% of the pulmonary roof length
Secondary ureter	Closed	Closed	Closed	Closed	Open all along rectum	Closed	Closed	Open all along rectum length
Pulmonary roof	Extends beyond top of kidney	Extends beyond top of kidney	Extends beyond top of kidney	Extends beyond top of kidney	Extends beyond top of kidney	Not extending beyond top of kidney	Not extending beyond top of kidney	Extending beyond top of kidney
Penis-epiphallus	Reflexed	Reflexed	Not reflexed	Epiphallus reflexed over itself	Not reflexed ?	Not reflexed ?	Not reflexed	Not reflexed
Penial appendix	Absent	Absent	Absent	Absent	Absent	Absent	Absent	Present
Length of bursa copulatrix	Less than half spermoviduct length	Extends to base of spermoviduct	Long, extends all spermoviduct length	Less than half spermoviduct length	Long, extends almost all spermoviduct length	Less than half the spermoviduct length	Less than half the spermoviduct length	Long, as long as spermoviduct
Length of diverticulum	Half spermoviduct length	Same length as bursa copulatrix sac	Half the bursa copulatrix length	Long, same length as spermoviduct	Short projection	Half the length of the bursa copulatrix	Half the length of the bursa copulatrix	¾ of the bursa copulatrix length
Verge	Absent	Absent	Absent	Present	Present	Present	?	Absent

Table 2
Continued.

Characters	<i>Solaropsis chicomendesi</i> , sp.nov.	<i>Solaropsis heliaca</i> (d'Orbigny, 1835)	<i>Solaropsis brasiliiana</i> (Deshayes, 1832)	<i>Solaropsis angulifera</i> Haas, 1955	<i>Solaropsis undata</i> (Lignitfoot, 1786)	<i>Solaropsis marmatensis</i> (Pfeiffer, 1854)	<i>Solaropsis nubeculata</i> (Deshayes, 1831)	<i>Solaropsis gibboni</i> (Pfeiffer, 1846)
Penis sculpture	Pilaster and transverse undulating folds	Proximal portion with zigzag ridges, distal with straight ridges	Longitudinal ridges	Pilaster and longitudinal undulating folds	6 pilasters	Proximal portion with pilasters, distal portion with thin longitudinal folds	Proximal portion with pilasters, distal portion with thin longitudinal ridges in zigzag	Proximal portion with pilasters, distal portion with thin longitudinal folds
Female portion of the sperm-oviduct	Transversally plicated	Longitudinally plicated	Longitudinally plicated	Transversal sacculations	Longitudinally plicated	Transversally sacculated	Transversally sacculated	Longitudinally folded
Flagellum	Short and thick	Short and thick	Thin and long	Short with lateral projections	Short and thick	Thin, medium length	Thin, medium length	Thick and short
Free oviduct	Inserting in vagina in an angle, bursa copulatrix duct continuous with vagina	Continuous with vagina, bursa copulatrix duct inserts in an angle	?	Continuous with vagina, bursa inserts in an angle	Continuous with vagina, bursa inserts in an angle	Continuous with vagina, bursa inserts in an angle	Continuous with vagina	Continuous with vagina

fused with left parietal ganglion; all other ganglia of ventral chain in contact but not fused.

Etymology: This species is named to honor Francisco Alves Mendes, known as Chico Mendes, the brave defender of the tropical rainforest and its inhabitants.

DISCUSSION

Solaropsis is a poorly known genus of the neotropical malacological fauna. Most of the species comprising the genus (see Richardson, 1985) were described on the basis of shell characters. Tillier (1980) was the first to attempt to define *Solaropsis* using characters from the pallial and genital system. Later, the diagnosis for the Solaropsidae proposed by Nordsieck (1986) was based on three main characters: diverticulum present (bursa copulatrix), male duct with penial appendix, and forked penial muscle retractor. While these characters are present in the type species of *Solaropsis*, only the presence of a diverticulum in the bursa copulatrix is a constant character in the rest of species with known anatomy in the genus. Also, *Solaropsis* is morphologically similar to *Labyrinthus* and *Isomeria* in shell sculpture, the presence of a reflexed penis-epiphallus, the length and morphology of the kidney, and the length of the typhlosole in the digestive system. For this reasons, *Solaropsis* should be classified within the Camaenidae, at least until additional anatomical information is available, and a phylogenetic analysis of the Camaenidae is carried out, supporting its inclusion or exclusion from that family.

Three characters that are common to all the species of *Solaropsis* anatomically studied are: (1) the presence of a bifurcated bursa copulatrix duct; (2) a spermoviduct groove extending through the free oviduct; and (3) the long typhlosole in the intestine. However, only a cladistic analysis of the genus can determine if those characters are indeed true synapomorphies of the genus.

Different anatomic characters of *S. chicomendesi* were compared (Table 2) with species with studied anatomy except for *S. feisthameli*, which was poorly described by Von Ihering (1900).

With regard to its shell, *S. chicomendesi* does not present the deep constriction on the peripheral portion of the body whorl, which is often present in some specimens of the type species, *S. undata*. *S. chicomendesi* shares a similar pattern of shell sculpture with most of the *Solaropsis* described except for *S. gibboni* where the granules of the shell are absent.

The pallial system is similar in all *Solaropsis* studied, except for the kidney length which is less than half the pulmonary roof length in *S. gibboni* and *S. undata*; the other species show a very long kidney, about 80% the length of the pulmonary roof length. The secondary ureter is open only in *S. undata* and *S. gibboni*, being closed until the distal portion of the rectum in the other species.

The radula is similar in all species studied and does

not seem to be an important character in distinguishing *Solaropsis* species. The jaw is ribbed in all species and particularly thin in *S. chicomendesi* and *S. feisthameli*.

With regard to the reproductive system of *S. chicomendesi*, the reflexed penis-epiphallus is present in some species of *Solaropsis* such as *S. angulifera*, *S. heliaca*, and *S. chicomendesi*, although some differences exist among them. In the case of *S. angulifera*, the epiphallus is reflexed over itself, whereas in the other two, the epiphallus is reflexed over the penis. The ovotestis in all species studied is formed by a unique mass of round to oval acini. As in most American Camaenidae the FPSC in *S. chicomendesi* is not evident and is probably absent as in the rest of *Solaropsis* species. The presence of a diverticulum in the bursa copulatrix is a character constant in the genus. In *S. chicomendesi* the free oviduct inserts into the vagina in an angle while the vagina is continuous with the bursa copulatrix duct. This situation is very peculiar since in the majority of Stylommatophoran snails the free oviduct is continuous with the vagina, whereas the bursa copulatrix duct usually inserts in an angle in the vagina. Only in *Labyrinthus* and *Isomeria* species has a similar disposition of the organs and ducts been described (Solem, 1966; Cuezzo, in press). In the rest of *Solaropsis* species the free oviduct is continuous with the vagina.

Solaropsis is probably more related to the Camaenidae than to any other Stylommatophoran family because it shows several morphological similarities with the other continental Camaenidae: *Labyrinthus* and *Isomeria*. However, only through a cladistic analysis will it be possible to test this hypothesis. The three mentioned genera are poorly known so it is urgent that new collections of live material be carried out, as well as more anatomical studies to permit generic systematic revisions. This goal can only be realized through support for training in taxonomy of young local malacologists in different countries where the malacological fauna is so poorly known.

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NOTES, INFORMATION, & NEWS

**Rediscovery of “*Actaeon*” *secale* Gould, 1859
(Gastropoda: Architectibranchia: Acteonidae) from
Yanai, Yamaguchi Prefecture, Japan**Hiroshi Fukuda¹, Shigeo Hori² and Reiko Kuroda^{2,3}¹ Department of Conservation of Aquatic Ecosystems,
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“*Actaeon*” *secale* Gould, 1859, is a species of the primitive opisthobranch family Acteonidae which was described from “China Seas” by Gould (1859:142; 1862: 113). Photographs of the holotype specimen (deposited in the U.S. National Museum) were published by Yen (1944: 577, pl. 51, fig. 32) and Johnson (1964:147, pl. 12, fig. 4). However, this species has not been recorded independently since its original description either from the coast of China (Lin, 1997) or Japan (Higo et al., 1999).

Wada et al. (1996) included “*Punctacteon kawamurai* (Habe, 1952)” in the World Wide Fund for Nature (WWF) Japan’s red data book for organisms living in the inner bays of Japan, citing it as “rare,” and stated “occurs on mud flats in the subtidal zone of the innermost part of bays; several living specimens have recently been found in Nabeta Bay, Shimoda City, Shizuoka Prefecture and Yanai Bay, Yamaguchi Prefecture.”

Recently we re-examined the voucher specimens of “*P. kawamurai*” sensu Wada et al. (1996) from Yanai Bay (two empty shells and 11 fragments, deposited in the Yamaguchi Museum, no. YMZ-Mo 6005; Figures 1–5). They were originally collected by one of the present authors (H. F.) from a sediment bottom in the subtidal zone (about 10 m depth) of Yanai Bay in 1990, along with some specimens of *Lucidesta mundula* (A. Adams, 1860), *Iravadia (Pseudonoba) bella* (A. Adams, 1853), *I. (P.) yendoi* (Yokoyama, 1927), and *Japanonoba patula* (A. Adams, 1863) [as *J. itoi* Habe & Andô, 1987], all of which were illustrated by Wada et al. (1996).

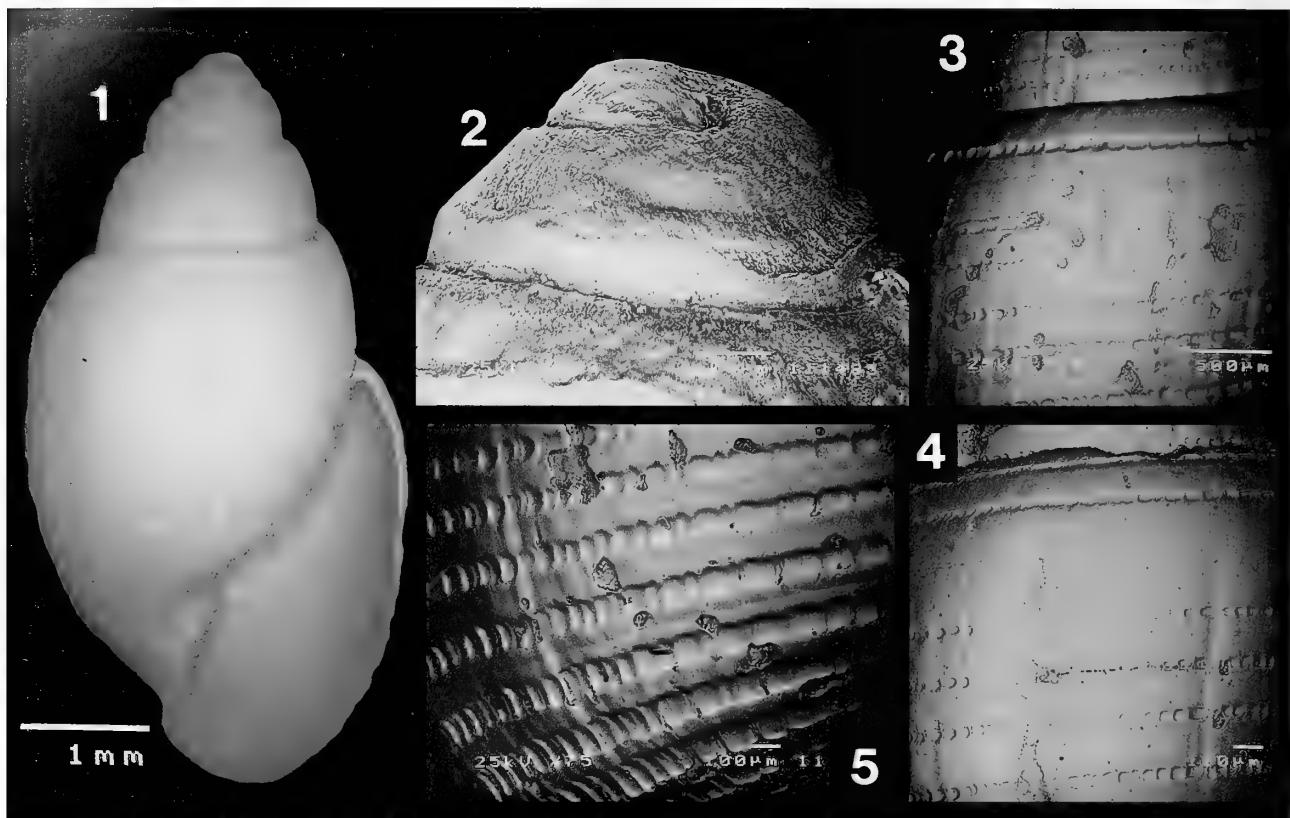
Re-examination revealed that the “*P. kawamurai*” from Yanai Bay is not *P. kawamurai* but “*A.*” *secale*. This is the first rediscovery of “*A.*” *secale* after a hiatus of about 140 years since the original description. Here we redescribe the shell of “*A.*” *secale* based on the specimens from Yanai Bay.

The shell (Figures 1–5) is small (height × diameter of two complete specimens: 5.55 × 2.90 mm and 4.65 × 2.30 mm), pupiform, polished and opaque, ivory in color. The protoconch (Figure 2) is clearly heterostrophic, but sufficiently eroded in the present specimens that the number of whorls, the angle of the protoconch axis to the teleoconch axis, and the sculpture of the surface could not be determined. The teleoconch consists of about four to five weakly convex whorls with weakly impressed sutures. Weak, irregular growth lines are present on each whorl, and the majority of the shell surface bears conspicuous, punctate spiral grooves (16 to 20 on the body whorl); the interspaces form spiral ribs and are one to three times as wide as the spiral grooves. Just abapical to the sutures of each teleoconch whorl one or two distinct spiral grooves are present, but there is an area of only extremely weak spiral grooves abapical to the first or second subsutural spiral grooves; the area is as wide as three to five sets of the abapical spiral grooves and their interspaces (Figures 3, 4). The rest of each whorl bears conspicuous spiral grooves, becoming stronger and wider with narrower interspaces toward the base (Figure 5). One of the present specimens bears indistinct pink spiral bands on the base of the last whorl and around the shoulder of each whorl. The columella is slightly curved and covered with a thin callus, with a moderate fold at its abapical part. There is no umbilicus. The outer lip is thin.

Originally, this species was described as a member of *Actaeon* (= *Acteon* Montfort, 1810) by Gould (1859, 1862). This species bears, however, distinct punctate spiral grooves unlike the type species of *Acteon*, *A. tornatilis* (Linnaeus, 1758), on which the spiral grooves are simple and obsolete. The features of “*A.*” *secale* match those of the type species of *Punctacteon* Kuroda & Habe in Habe, 1961. *P. fabreana* (Crosse, 1874). For this reason, this species is here placed in *Punctacteon* (comb. nov.).

This species was cited as *P. kawamurai* by Wada et al. (1996). However, *P. kawamurai* (see clear photograph by Tsuchida & Hori, 1996: pl. 3, fig. 7) differs from this species in having broader and deeper spiral grooves with narrower interspaces, and in lacking the weakly grooved area on the subshoulder, which is the most distinct character of *P. secale*. Furthermore, *P. kawamurai* inhabits sea bottom of 93–97 m (Tsuchida & Hori, 1996) or 100–200 m deep (Higo et al., 1999), whereas *P. secale* from Yanai Bay was collected from only about 10 m.

Punctacteon kawamurai should be eliminated from the red data book of the Japanese animals of inner bays, and *P. secale* should be added to it instead of *P. kawamurai*. Also, the specimens of “*P. kawamurai*” from Nabeta



Figures 1–5. *Punctacteon secale* (Gould, 1859). Yanai Bay, Yamaguchi Prefecture, Japan (YMZ-Mo 6005). 1. Ventral view of the whole shell. 2. Protoconch. 3, 4. Sculpture on the subshoulder. 5. Sculpture on the base.

Bay, Shimoda City, Shizuoka Prefecture by Wada et al. (1996) would need to be reviewed.

Acknowledgments. We would like to thank Dr Hiroshi Saitō (National Science Museum, Tokyo) who kindly assisted our examination with low-vacuum SEM. Mr Paul Callomon (Elle Scientific Publications) patiently helped us with the English language.

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A New Genus of Aporrhaid Gastropod from Upper Paleocene Rocks in Southern California

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The family Aporrhaidae Gray, 1850, is a group of marine gastropods characterized by a highly modified apertural margin. It apparently originated near the end of the Triassic and was an important component of the late Mesozoic marine-gastropod fauna (Roy, 1994). The end-Cretaceous mass-extinction removed about 76% of the aporrhaid genera (Roy, 1996).

On the Pacific slope of North America, early Tertiary (Paleogene) aporrhais represent a very minor component of the molluscan fauna. Aporrhais previously reported from this region are *Araeodactylus* (?) *costatus* (Gabb, 1869), *Tessarolax* (?) *inconspicua* (Gabb, 1869), *Drepanocheilus exilis* (Gabb, 1864), and *Drepanocheilus* (?) *transversus* (Gabb, 1869). All of these species, which are illustrated by Stewart (1927), are late Paleocene in age and from California (Stewart, 1927; Weaver, 1953; Zinsmeister, 1983). The latter species is also known from upper? Paleocene rocks in Baja California, Mexico (Zinsmeister & Paredes, 1988). *Tessarolax* (?) *inconspicua* is based on poorly preserved material and might not even be an aporrhaid. *Drepanocheilus exilis* and *Drepanocheilus* (?) *transversus* are also based on incomplete specimens, and future collecting might possibly reveal them to be conspecific.

Recent collecting in upper Paleocene rocks in southern California revealed a single specimen of a very rare aporrhaid that represents a new genus. This new gastropod, *Spinigeropsis*, differs from most other aporrhais by having digitations on both sides of the shell rather than only on one side. The specimen of the new gastropod was found at LACMIP locality 16869 in the upper part of the Santa Susana Formation in the Palisades Highlands area just east of Santa Ynez Canyon in the east-central Santa Monica Mountains, Los Angeles County, southern California (Figure 1). This locality is in a richly fossiliferous lens within a very fine-grained sandstone approximately 20 m stratigraphically below an algal-limestone interval. This locality and others in the immediate area are in rocks of late Paleocene age (Thanetian Stage) which were deposited in a protected bay (no deeper than 40 to 70 m) with warm-water, algal-limestone buildups associated with shoals on the bay floor (Squires & Kennedy, 1998).

The following institutional acronym is used: Natural History Museum of Los Angeles County, Section of Invertebrate Paleontology, Los Angeles (LACMIP).

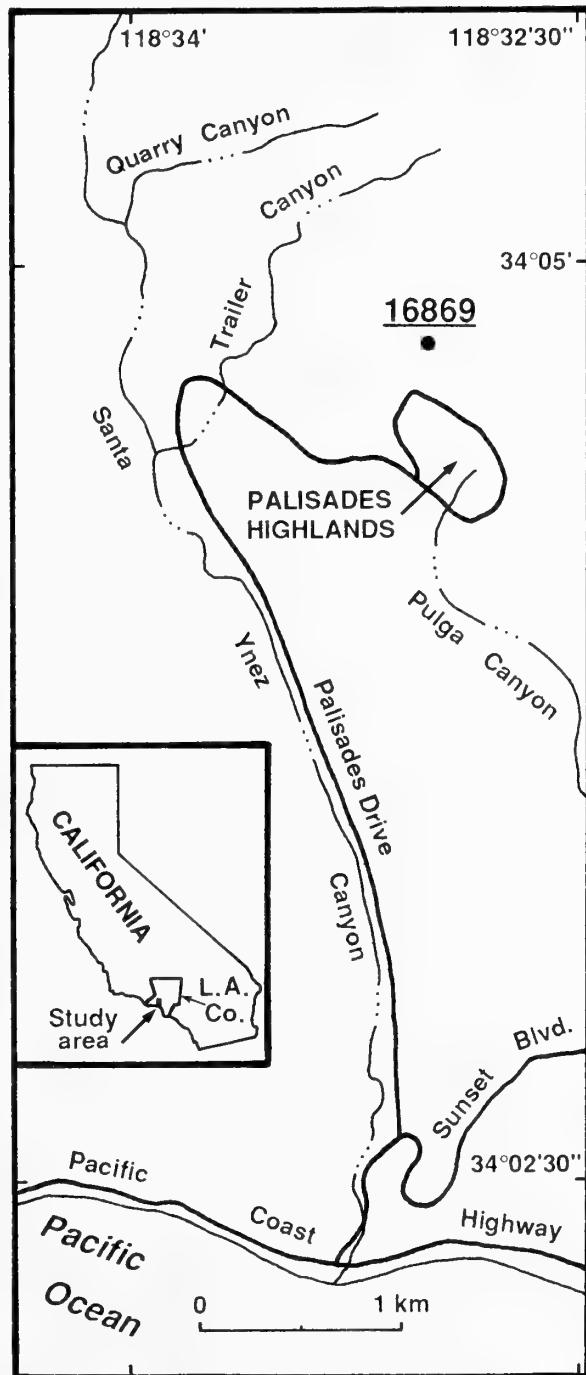
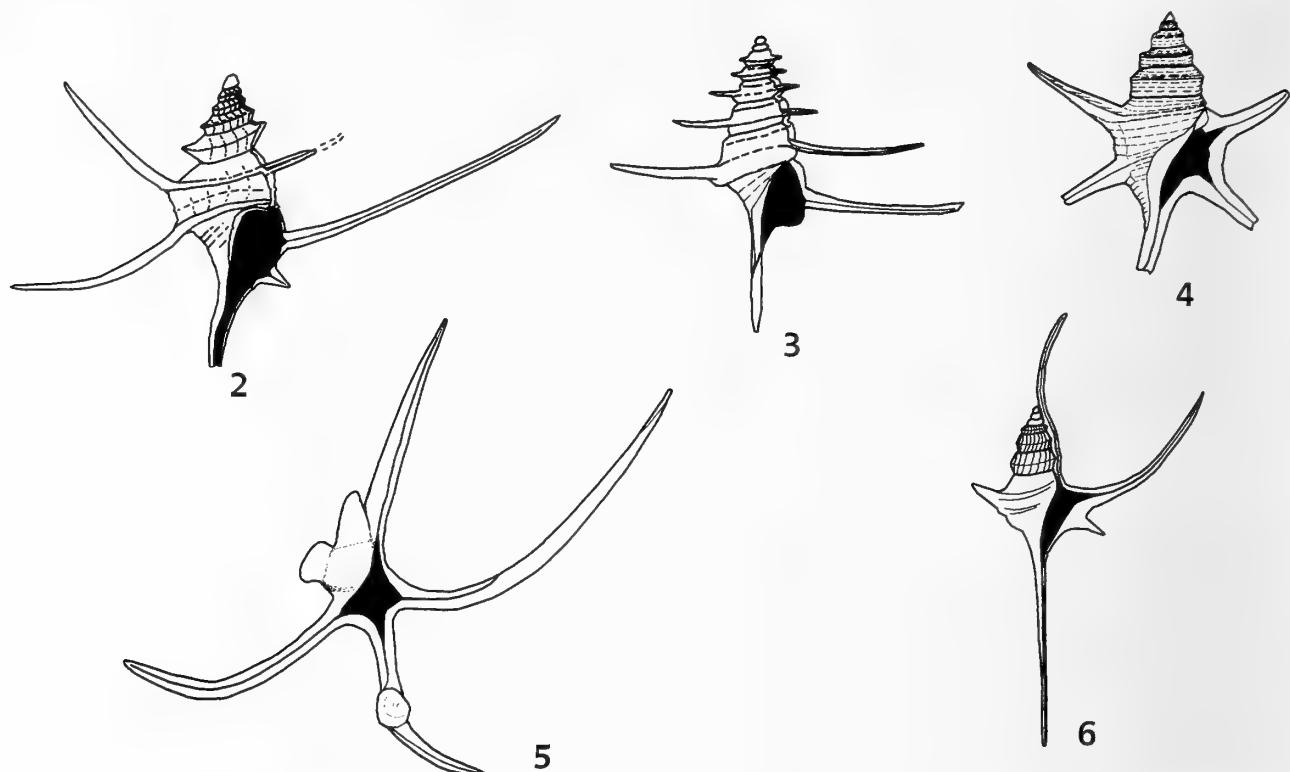


Figure 1. Index map showing type locality of new species in the upper part of the Santa Susana Formation, Palisades Highlands, east-central Santa Monica Mountains, Los Angeles County, southern California (from Squires & Kennedy, 1998).



Figures 2–6. Morphologies of aporhaid genera similar to the new genus. All are apertural views; Figure 3 from Wenz (1940), Figure 4 from Cossmann (1904), Figure 5 from Saul (1989), and Figure 6 adapted from Loch (1989). Figure 2. *Spinigeropsis* Squires & Saul, gen. nov., $\times 2.4$. Figure 3. *Spinigera* s. s., $\times 1$. Figure 4. *Spinigera* (*Diempiterus*), $\times 1$. Figure 5. *Tessarolax*, $\times 0.5$. Figure 6. *Teneposita*, $\times 1$.

Systematic Paleontology

Class GASTROPODA Cuvier, 1797

Superorder CAENOGASTROPODA Cox, 1959

Family APORRHAIDAE Gray, 1850

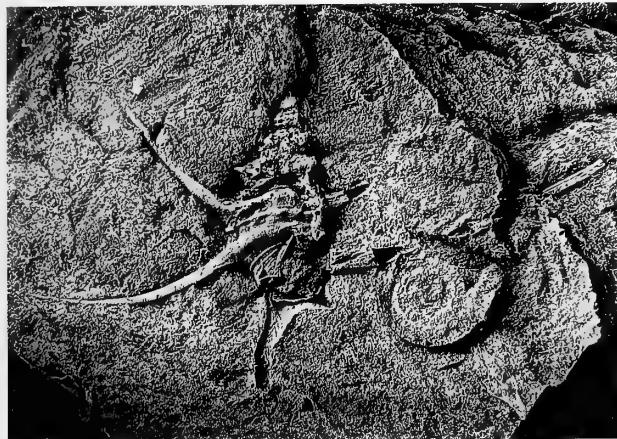
Genus *Spinigeropsis* Squires & Saul, gen. nov.

Type species: *Spinigeropsis calafia*, sp. nov.; late Paleocene, southern California.

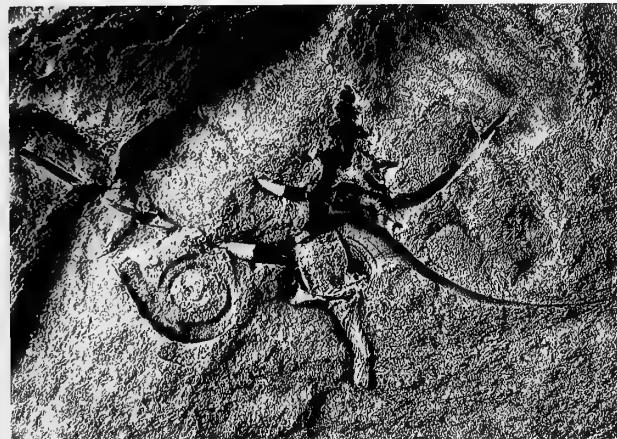
Diagnosis: Small aporhaid with two opposing digitate varices (on left and right sides of shell), both extending onto spire; digitations at intersections of varix and strong anterior and posterior spiral cords; on spire whorls a short digitation on each side; on body whorl two very long, narrow, delicate, and spinelike digitations on outer lip and opposite whorl side; rostrum moderately short and bent.

Discussion: Previously known aporhoids that have unwebbed digitations on both sides of the shell (Figures 3–7) are *Spinigera* (*Spinigera*) d'Orbigny, 1850, *Spinigera* (*Diempiterus*) Piette, 1876, *Tessarolax* Gabb, 1864, and *Teneposita* Loch, 1989. Of these four aporhoids, *Spinigeropsis* most closely resembles *Spinigera* (*Diempiterus*) from Jurassic strata of Europe. Roy (1994) reported the

geologic range of *Diempiterus* as Middle Jurassic (Bathonian Stage) to Late Jurassic (Kimmeridgian Stage). *Spinigeropsis* differs from *Diempiterus* by having axial ribs and varices on the spire, short digitations on the spire, a more posteriorly directed digitation on the left-side shoulder of the body whorl, and a seemingly more equant aperture. *Spinigeropsis* differs from *Spinigera* s.s. by having no digitations on uppermost spire, shorter digitations on middle part of spire, two rather than just a single digitation on left side of body whorl, posteriorly directed digitations, and a bent and much shorter rostrum. Roy (1994) reported the geologic range of *Spinigera* s.s. to be Middle Jurassic (Bajocian Stage) to Early Cretaceous (Hauterivian Stage). *Spinigeropsis* differs from the Late Cretaceous genera *Tessarolax* and *Teneposita* by having varices on the spire, two digitations on the left side of the body whorl rather than one, a shorter rostrum (especially compared to *Teneposita*), and not having a posterior canal that extends beyond the apex. In addition, the length of the spire and body whorl of *Spinigeropsis* is much smaller than that of *Tessarolax* but slightly larger than that of *Teneposita*. Roy (1994) reported the geologic range of *Tessarolax* to be Early Cretaceous (Hauterivian Stage) to Late Cretaceous (Maastrichtian Stage). Loch



7



8

Figures 7, 8. Specimen coated with ammonium chloride. Figures 7, 8. *Spinigeropsis calafia* Squires & Saul, gen. & sp. nov., LACMIP holotype 12873, LACMIP loc. 16869, height 16.5 mm, $\times 2.4$. Figure 7. Apertural view (rubber peel of an external mold). Figure 8. Abapertural view (external mold).

(1989) reported the geologic range of *Teneposita* to be Late Cretaceous (late Campanian Stage to possibly early Maastrichtian Stage).

Etymology: The new genus is named for being similar to *Spinigera*.

Spinigeropsis calafia Squires & Saul, sp. nov.

(Figures 2, 7, 8)

Diagnosis: As for the genus.

Description: Shell small, fusiform, consisting of 6½ whorls; spire moderately high (about 30% of total shell height), apical angle 40°. Protoconch not preserved. Upper two spire whorls smooth (decorticated?), next two spire whorls cancellate with anterior one (antepentulti-

mate whorl) medially carinate; antepenultimate and all subsequent whorls with two varices, one on left side of shell and an opposite one on right side (outer lip side) of shell; digitations becoming stronger on each succeeding whorl, especially on body whorl. Penultimate whorl medially carinate with a short digitation on each varix. Body whorl tricarinate; cords on carinae, anterior and posterior cords strong, subequal middle cord about half as strong; posterior carina bearing two elongate and somewhat posteriorly directed, spinelike digitations at varices; medial carina with no digitations; anterior carina bearing two very elongate, slightly curved and laterally directed, spinelike digitations at varices. Neck of body whorl with several spiral ribs. Aperture quadrate, inner lip smooth with a thin border. Outer lip coincident with right varix bearing two spinelike digitations. Rostrum moderately short, slightly bent to right and bearing coarse growth lines.

Holotype: LACMIP 12873, 16.5 mm high (including spire and body whorl), 30 mm wide (including digitations).

Type locality: LACMIP loc. 16869, upper part of Santa Susana Formation, Santa Ynez Canyon area, east-central Santa Monica Mountains, Los Angeles County, southern California, latitude 34°4'43"N, longitude 118°33'03"W, U.S. Geological Survey, 7.5-minute Topanga Quadrangle, 1952 (photorevised, 1981).

Geologic age: Late Paleocene ("Martinez Stage," equivalent to Thanetian Stage).

Distribution: Known only from the type locality.

Discussion: A single specimen was found, and although it is mostly an external mold, it shows most of the long, delicate digitations on the body very well, whereas portions of the others are partly concealed by rock matrix.

The new species bears the closest resemblance to *Spinigera (Diempperterus) longueueana* (Piette, 1876), the type species of subgenus *Diempperterus*. Wenz (1940:fig. 2708) illustrated this French species and reported its geologic age as Late Jurassic (Kimmeridgian Stage). The new species differs from *S. (D.) longueueana* by having digitations on the spire, two digitations rather than one on the body whorl, cancellate ornamentation on the upper spire, a more anteriorly placed aperture, and the bases of the digitations on the outer lip much closer together.

As mentioned earlier, the only other aporrhoids known from the Paleogene rock record of the Pacific coast of North America are *Araeodactylus (?) costatus* (Gabb, 1869:167, pl. 28, fig. 48; Stewart, 1927:366, pl. 25, fig. 6), *Tessarolax (?) inconspicua* (Gabb, 1869:151, pl. 26, fig. 29; Stewart, 1927:365–366, pl. 23, fig. 2), *Drepanocheilus exilis* (Gabb, 1864:129, pl. 29, fig. 231) and *Drepanocheilus transversus* (Gabb, 1869:165, pl. 27, fig. 45; Zinsmeister & Paredes, 1988:pl. 1, fig. 9). *Araeodactylus*

(?) *costatus* differs from the new species by having an alate outer lip, no varices, and no axial ribs on the spire. *Tessarolax* (?) *inconspicua* differs from the new species in that it has no digitations and no varices. The two species of *Drepanocheilus* are also markedly different from the new species in that they possess an alate outer lip with a single digitation and spire ornamentation dominated by axial ribs.

Etymology: The new species is named for the state of California.

Acknowledgments. The specimen of the new species was found by Charles D. Burt, and William Rader facilitated the gift of the specimen to LACMIP. Lindsey T. Groves (LACMIP) helped in obtaining hard-to-find literature.

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BOOKS, PERIODICALS & PAMPHLETS

Panamic Province Molluscan Literature: Additions and Changes from 1971 through 2000. I. Bivalvia. II. Polyplacophora

by CAROL SKOGLUND. The Festivus 32, Supplement:i–v, 1–119 (part I); I, 1–20 (part II). Available from San Diego Shell Club, 3883 Mt. Blackburn Ave., San Diego, CA 92111, USA. \$US 22.00 within United States; \$25.00 (surface mail) or \$30.00 (airmail) to destinations outside the United States.

This solidly spiral-bound work updates sections of *Sea Shells of Tropical West America: Marine Mollusks from Baja California to Peru* (Keen, 1971) and supersedes earlier updates of the same work by Skoglund (1989, 1991). The two separate contained papers consolidate information on new taxa and synonymies, redefined taxonomic relationships, and geographic distribution for bivalves and chitons, respectively. Of the various suprageneric taxonomies published since 1971, this work follows Coan et al. (2000) to the extent possible for the bivalves, and Van Belle (1999) for the chitons. Only those species with published changes since 1971 are included. Synonyms are listed as published by each author; where there is disagreement, both versions are shown and the reader is en-

couraged to use his or her own due diligence—using the extensive Literature Cited—in making a choice between them. The work is a largely objective report and analysis of the taxonomic and biogeographic work that has taken place in the province over the last 30 years and should be welcomed as a research tool by all persons with interests in tropical marine mollusks.

B. Roth

Literature Cited

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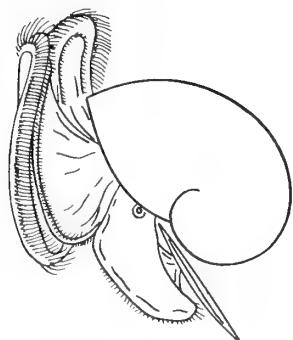
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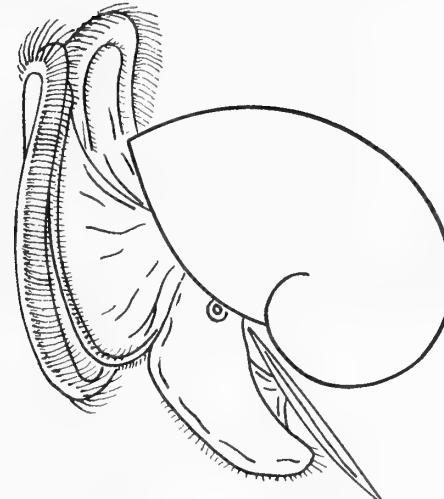
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Hatching Depth of *Nautilus pompilius* in Fiji

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Abstract. Analyses of oxygen and carbon isotopes in the shell and septa of *Nautilus* have shed light on the early life history of this animal. Previous studies have shown that $\delta^{18}\text{O}$ is a reliable indicator of the temperature and, by inference, the depth at which the shell material forms. Thus, it is clear that *Nautilus* hatches at 22–24°C, corresponding to a depth of 100–200 m, depending on the location; thereafter, animals migrate to colder, deeper water (300–400 m depth). However, Davis & Mohorter (1973) reported the capture of three specimens of newly hatched *Nautilus* in shallow water (1.25 m deep) in Korolevu Bay, Viti Levu, Fiji. To resolve this paradox, we analyzed the isotopic composition of the septa and apertural margin in two of these specimens. The specimens are approximately 25 mm in diameter and show the neopionic constriction on the outer shell and a reduction in septal spacing, features that indicate the point of hatching. The oxygen isotope values of the embryonic septa in both specimens range from –0.77 to –0.55‰, corresponding to an average temperature of 22.6°C and a depth of 160 m (based on temperature-depth profiles in the area). The values of $\delta^{18}\text{O}$ of the postembryonic septum and apertural margin are 1.33 and 0.99‰, respectively, in one specimen (corresponding to 14°C, 370 m depth), and 0.42 and 0.53‰, respectively, in the other specimen (corresponding to 17°C, 300 m depth). The values of $\delta^{13}\text{C}$ also show a marked difference between embryonic and postembryonic shell material (–0.82 to 0.67‰ in embryonic and –2.40 to –1.06‰ in postembryonic shell material). Thus, these animals did not hatch in shallow water, but exhibited the same pattern as that of other *Nautilus* from Fiji: hatching at a depth of 160–210 m, followed by a descent to a depth of 300–370 m. Thereafter, these animals apparently migrated or were transported (by currents?) to shallow water where they were captured; the geographic distance involved was 1.5 km (based on bathymetric charts). Reports of drifted shells of approximately the same size collected in the same area and elsewhere indicate that this post-hatching behavior may not be uncommon and may well be fatal.

INTRODUCTION

Davis & Mohorter (1973) reported the capture of three small juveniles of *Nautilus* in Korolevu Bay on the southwest coast of Viti Levu, Fiji (Figure 1). The specimens are approximately 25 mm in diameter and, on the basis of their morphological features, appear to have been newly hatched (Figure 2). What is astonishing is the shallow depth at which these animals were collected—only 1.25 m. That report constitutes the only published account of newly hatched *Nautilus* in the wild.

The implication of this finding was that the animals had hatched in shallow water. Nevertheless, this occurrence was considered anomalous. Chamberlain (1978) doubted that juvenile *Nautilus* could survive the turbulence in such shallow water. Ward & Martin (1980) argued that the temperatures near the surface would be lethal to young animals. In addition, they reasoned, if breeding and hatching occur in shallow water, why had they and others failed to find more animals at those depths during subsequent searches. Moreover, one of us (R. A. D.) visited Korolevu and interviewed local inhab-

itants, none of whom could recall seeing small individuals of *Nautilus*.

In the two decades after the Mohorter specimens were collected, studies of the carbon and oxygen isotope record of *Nautilus* shed new light on the question of hatching depth (Eichler & Ristedt, 1966a, b; Cochran et al., 1981; Taylor & Ward, 1983; Oba & Tanabe, 1983; Oba et al., 1992). These studies revealed a characteristic pattern of light $\delta^{18}\text{O}$ values for embryonic septa followed by a marked shift toward heavier values for postembryonic septa.

To help explain this pattern, Landman et al. (1994) analyzed the isotopic record in *Nautilus belauensis* Saunders, 1981, raised in aquaria under controlled temperature conditions. They concluded that both the embryonic and postembryonic septa of *Nautilus* are secreted with the same temperature-dependent fractionation of aragonite relative to water as that of other aragonite-secreting mollusks (Grossman & Ku, 1986). The $\delta^{18}\text{O}$ values of the septa thus provide a reliable means of determining the water temperature, and, by inference, the depth at which the septa form.

Using the results of this study, Landman et al. (1994)

interpreted the oxygen isotope patterns of specimens caught in the wild. These analyses indicated that hatching occurs at 22–24°C, corresponding to a depth of 100–200 m, depending on the location. In particular, in Fiji, it occurs at an average temperature of 22°C, corresponding to a depth of about 190 m. The abrupt increase in $\delta^{18}\text{O}$ observed in postembryonic septa reflects migration to colder, deeper water after hatching.

In light of these data, we investigated the record of carbon and oxygen isotopes in the specimens described by Davis & Mohorter (1973). The specimens are deposited in the Cincinnati Museum of Natural History (CMNH), and permission was obtained to sample them for isotopic analyses.

BACKGROUND

Davis & Mohorter (1973) described three specimens of *Nautilus* from Fiji (CMNH 74-103 A–C), which they referred to as *Nautilus* cf. *N. pompilius* Linnaeus, 1758. In the intervening years, many studies have demonstrated that the only species of *Nautilus* present in Fiji is *N. pompilius* (see Ward & Martin, 1980; Ward, 1987; House, 1987; Hayasaka et al., 1987; Saunders, 1987; Saunders & Ward, 1987; Tanabe et al., 1990). We therefore regard these specimens as *N. pompilius*, although it is difficult to differentiate juvenile shells of the various species of *Nautilus* purely on the basis of morphology or color.

Of the three specimens, two were caught between February 22 and the end of March, 1955 in the lagoon behind the barrier reef in Korolevu Bay, Viti Levu (Figure 1, A on map). They were found in a hole in a submerged rock at a depth of about 1.25 m. The third specimen was caught between January 1 and February 2, 1958, also in a hole in a submerged rock in Korolevu Bay (Figure 1, B on map). Unfortunately, which specimen was collected where was not recorded at the time the specimens were captured.

At the mouth of Korolevu Bay, there is a break in the barrier reef 0.3 km wide. On the seaward side of the reef, the water deepens rapidly, attaining a depth of 1000 m in a distance of 3 km (slope = 18°) (Holmes, 1982). Ward et al. (1977) and Hayasaka et al. (1987) described similar steep submarine slopes off Suva on the southeast coast of Viti Levu.

We analyzed specimens 74-103 B and C (Figures 2A–D; see Davis & Mohorter, 1973:table 1). Specimen 74-103B is 26.1 mm in diameter, with nine septa and a reduction in septal spacing (septal approximation) between septa 8 and 9. Specimen 74-103C is 23.2 mm in diameter, with eight septa and a reduction in septal spacing between septa 7 and 8. Both specimens show the nepionic constriction just adapical of the apertural margin.

The reduction in septal spacing coincides in time of formation with the growth discontinuity (nepionic constriction) at the aperture, and both features demarcate the

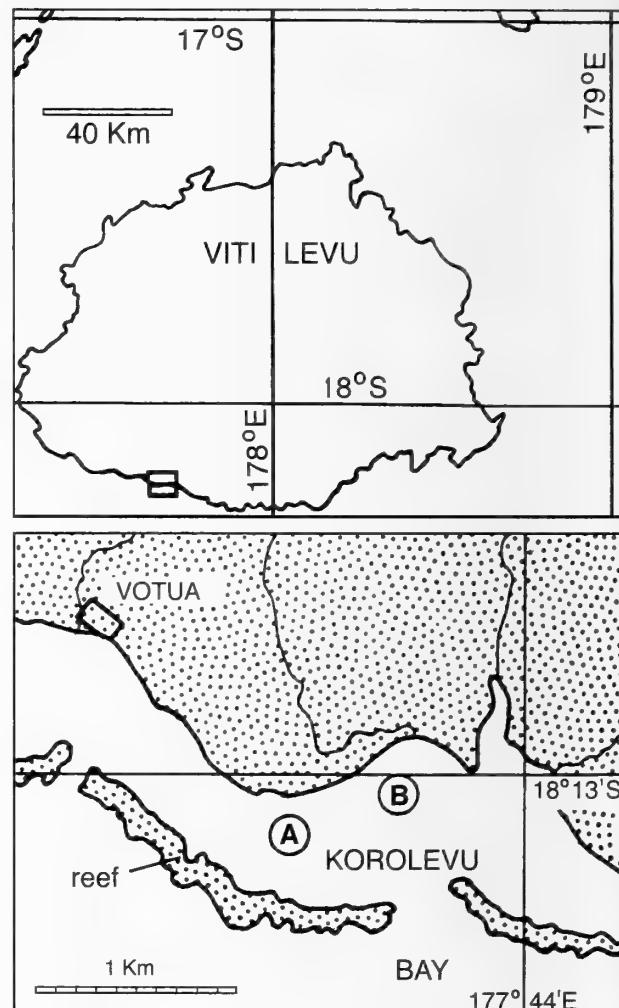


Figure 1. Index map (top) and close-up (bottom) of part of the Fiji Islands showing the localities (A, B) where the specimens of *Nautilus pompilius* Linnaeus, 1758, were captured. (Modified from Davis & Mohorter, 1973:fig. 1).

point of hatching on the shell (Arnold et al., 1987; Landman, 1988; Landman et al., 1994). Thus, specimen 74-103B hatched between septa 8 and 9, and septa 1–8 formed during embryonic development, and septum 9, during postembryonic development. Specimen 74-103C hatched between septa 7 and 8, and septa 1–7 formed during embryonic development, and septum 8, during postembryonic development. The outer shell grew slightly beyond the nepionic constriction in both specimens.

METHODS

Specimens were sectioned along the medial plane, and the septa were sampled for analysis. In addition, we sampled a small piece of shell at the apertural margin in each specimen. The samples, consisting of tiny pieces of aragonitic shell material, were crushed into coarse powders.

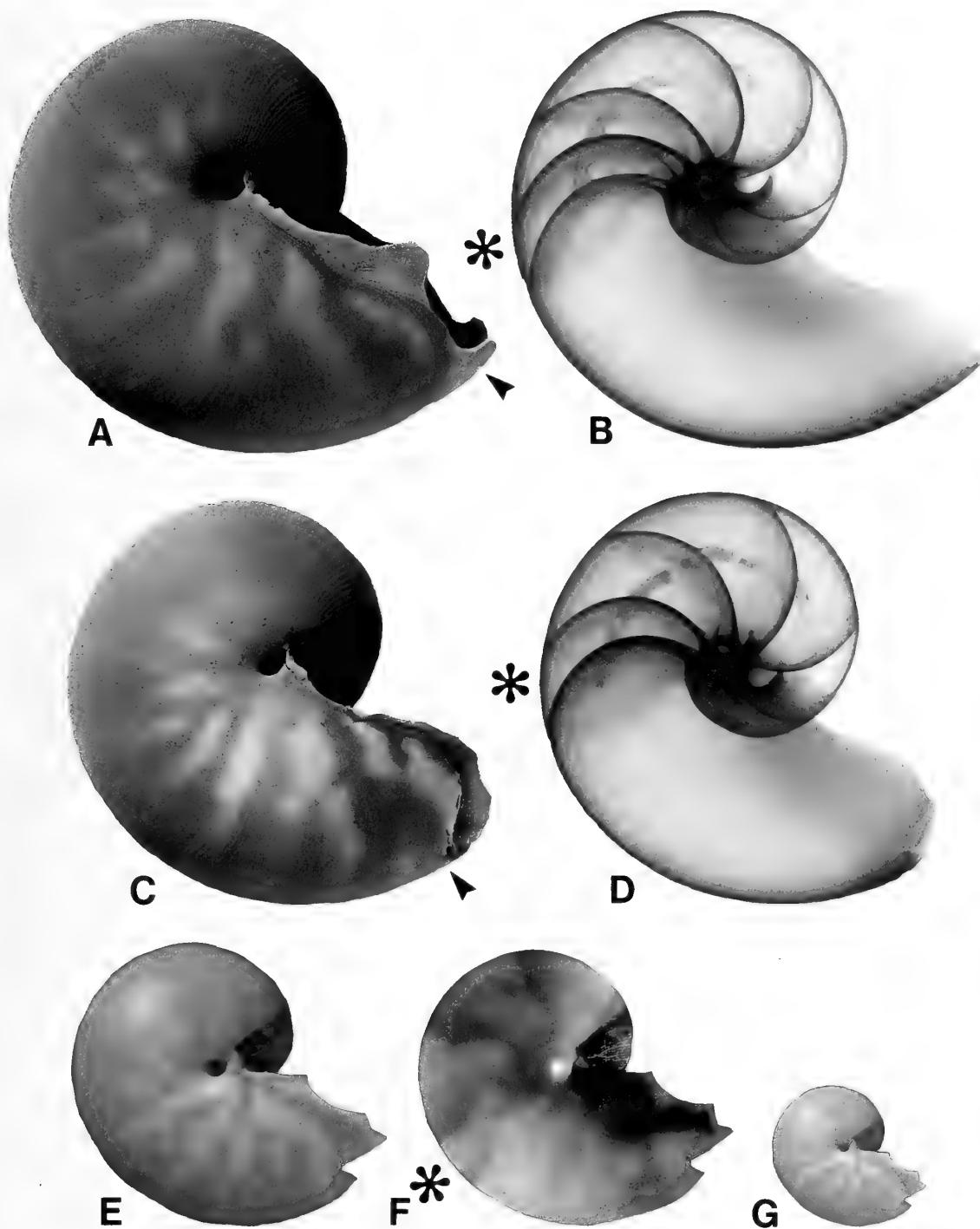


Figure 2. A, B. *Nautilus pompilius* Linnaeus, 1758, CMNH 74-103B, live-caught, Korolevu Bay, Fiji, diameter 26.1 mm. A. Right lateral view. B. Right lateral view, x-ray. C, D. *Nautilus pompilius*, CMNH 74-103C, live-caught, Korolevu Bay, Fiji, diameter 23.2 mm. C. Right lateral view. D. Right lateral view, x-ray. E-G. *Nautilus pompilius*, AMNH 44681, collected on the beach, Philippines, diameter 23.4 mm. E. Right lateral view. F. Right lateral view, transmitted light. G. Right lateral view. Arrows indicate the neponic constriction; asterisks, septal approximation.

Table 1

Stable isotope data for the septa and apertural margin in two live-caught *Nautilus pompilius* Linnaeus, 1758, from Fiji. Temperatures of the water in which the shell material formed are based on the equation of Grossman & Ku (1986) for the temperature-dependent fractionation of aragonite in mollusks relative to seawater. Septa are numbered in their order of secretion.

Specimen	Septum	$\delta^{18}\text{O}$	$\delta^{13}\text{C}$	T(°C)
74-103B	1	-0.59	-0.08	22.30
74-103B	2	-0.64	-0.31	22.57
74-103B	3	-0.64	0.00	22.54
74-103B	4	-0.77	0.20	23.17
74-103B	5	-0.67	0.53	22.69
74-103B	6	-0.56	0.67	22.19
74-103B	7	-0.71	0.37	22.90
74-103B	8	-0.63	0.03	22.48
74-103B	9	1.33	-1.06	13.29
74-103B	aperture	0.99	-2.10	14.92
74-103C	1	-0.75	-0.82	23.05
74-103C	2	-0.67	-0.30	22.67
74-103C	3	-0.73	-0.15	22.99
74-103C	4	-0.61	-0.05	22.40
74-103C	5	-0.57	0.26	22.22
74-103C	6	-0.55	0.10	22.12
74-103C	7	-0.68	-0.14	22.75
74-103C	8	0.42	-1.29	17.58
74-103C	aperture	0.53	-2.40	17.08

The powders were cleaned using the hydrogen peroxide procedure outlined by Allmon et al. (1992) to remove organic contaminants. The cleaned samples were then analyzed according to standard techniques (McCrea, 1950) involving an initial reaction in vacuo with 100% orthophosphoric acid at 90°C for 0.25 hr. An on-line, automated carbonate preparation system facilitated the production and purification of the evolved CO₂ gas. The isotopic differences between the derived samples of CO₂ and the PeeDee belemnite (PDB) standard were determined using the mass spectrometers in the Stable Isotope Laboratory in the Department of Geology at the University of Florida, Gainesville. Values of $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ are reported relative to the PDB standard, and the precision ranges from 0.05‰ to 0.10‰.

RESULTS

The results of the isotopic analyses are listed in Table 1 and illustrated in Figure 3. The oxygen isotope values of the embryonic septa in the two specimens range from -0.77 to -0.55‰. In contrast, the values of $\delta^{18}\text{O}$ of the postembryonic septum and apertural margin are 1.33 and 0.99‰, respectively, in specimen 74-103B, and 0.42 and 0.53‰, respectively, in specimen 74-103C. The values of $\delta^{13}\text{C}$ also show a marked difference between embryonic and postembryonic shell material (-0.82 to 0.67‰ in

embryonic and -2.40 to -1.06‰ in postembryonic shell material).

DISCUSSION

According to Landman et al. (1994), both the embryonic and postembryonic septa of *Nautilus* are secreted with the same temperature-dependent fractionation of aragonite relative to water as that of other aragonite-secreting mollusks (Grossman & Ku, 1986). Therefore, it is possible to determine the temperature, and, by inference, the depth at which the shell material forms.

We used the equation derived by Grossman & Ku (1986) to determine temperature:

$$T(\text{°C}) = 21.8 - 4.69(\delta_{\text{Ar}} - \delta_w)$$

where T is the temperature in degrees Celsius, δ_{Ar} is the oxygen isotope composition of the aragonite, and δ_w is the oxygen isotope composition of the water as defined by Epstein & Mayeda (1953) and modified by Craig (1961). The value of δ_w in Fiji is presumed to be -0.28 (based on $\delta^{18}\text{O}$ [Standard Mean Ocean Water, SMOW] values of Oba et al. [1992] converted to δ_w according to the equation of Friedman & O'Neil [1977]).

The calculated temperatures for the two specimens are listed in Table 1 and plotted in Figure 4. The temperature of formation of the embryonic septa is remarkably uniform in both specimens, with an average of 22.6°C (SD = 0.33; n = 15). The calculated temperatures of formation of the postembryonic septum and apertural margin are 13.3°C and 14.9°C, respectively, in specimen 74-103B, and 17.6°C and 17.1°C, respectively, in specimen 74-103C.

We consulted temperature-depth profiles in the region of capture to determine the corresponding depths of shell formation. The best available data are those of Holmes (1982:fig. 3, probe 1) showing a profile off Somosomo Bay, 11 km east of Korolevu Bay, for August 11, 1982.

On the basis of these data, the embryonic septa in both specimens formed at a depth of 160 m. The temperatures of formation of the postembryonic septum and apertural margin correspond to a depth of 370 m (355–380 m) in specimen 74-103B and 300 m (300–310 m) in specimen 74-103C. These depth estimates are approximate because the temperature-depth profile we used does not match the actual time and site of capture, and because the calculated temperatures reflect averages over the time of formation of the shell material, implying that the corresponding depths also represent averages.

The pattern of $\delta^{13}\text{C}$ in the two specimens is also consistent with a change in depth. The values of $\delta^{13}\text{C}$ of the postembryonic septa and aperture in both specimens are markedly lighter than those of the embryonic septa (Table 1). This difference reflects the variation in $\delta^{13}\text{C}$ of the total dissolved inorganic carbon in the water column. The embryonic shell formed in shallow water that was de-

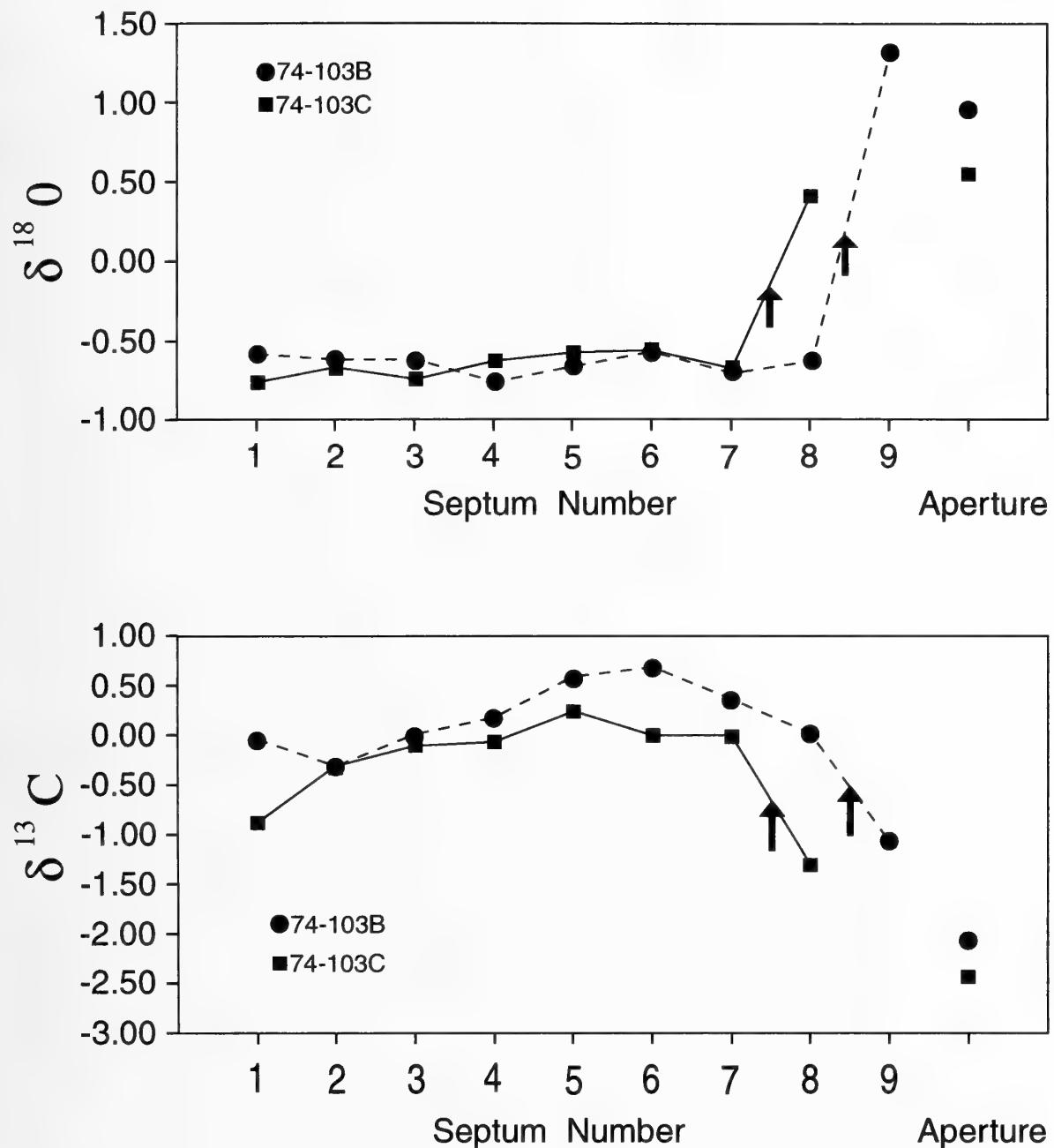


Figure 3. Values of $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ for samples of the septa and apertural margin in specimens 74-103B and 74-103C from Fiji. All values are relative to the PDB standard, and the precision ranges from 0.05‰ to 0.10‰. Septa are numbered in their order of secretion. The arrows indicate the point of hatching on each specimen.

pleted in ^{12}C by phytoplankton, whereas the postembryonic shell formed at greater depths where the $\delta^{13}\text{C}$ of the water (and hence the shell) was lighter due to regeneration of organic matter (Arthur et al., 1983).

Thus, these *Nautilus* did not hatch in the shallow lagoon in which they were collected. Instead, they must have followed the pattern inferred for other specimens

from Fiji: embryonic development and hatching at 21–23°C, corresponding to a depth of 160–210 m. After hatching, the animals descended to colder, deeper water (300–370 m deep).

There are several possible explanations for the presence of these animals in the lagoon. According to bathymetric charts (Holmes, 1982:fig. 2), the geographic dis-

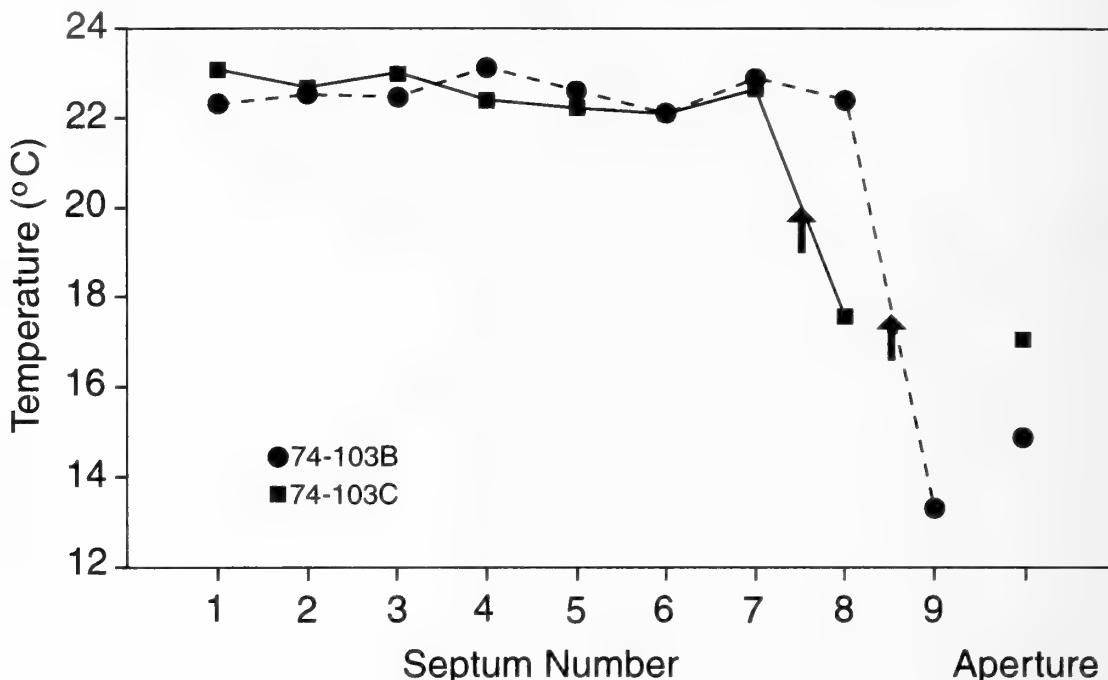


Figure 4. Calculated temperatures of the water in which the septa and apertural margin formed in specimens 74-103B and 74-103C. Septa are numbered in their order of secretion. The arrows indicate the point of hatching on each specimen.

tance between a depth of 370 m on the steep slope of the outer reef face and a depth of 1 m in the shallow lagoon near the site of capture is only 1.5 km.

One possibility is that storms transported the animals upslope. There is little meteorological information available for the time of capture of the specimens. However, Davis & Mohorter (1973) did not report any unusual weather conditions in the months prior to collection. In any event, it is unlikely that storms would have had any effects on water depths of as much as 370 m.

A second possibility is that the animals swam into shallow water. Diurnal migrations of *Nautilus* have been documented at several sites in the Pacific but not in Fiji. In Palau, *Nautilus* inhabit depths of 250–350 m during the day and migrate into shallower water (100–150 m deep) at night (Carlson et al., 1984; Ward et al., 1984). In New Caledonia, specimens have occasionally been caught at night at depths between 5 and 10 m (Ward & Martin, 1980). In Fiji, a few specimens have been caught at depths of as little as 100 m, but most have been caught in deeper water (Ward & Martin, 1980; Ward, 1987; Hayasaka et al., 1987).

The most likely explanation is that the newly hatched animals swam part way up the slope, perhaps to a depth of 100–200 m. Such small animals would not have been very powerful swimmers (Chamberlain, 1978), and upwelling currents then could have carried them the rest of the way through the passage in the reef into the shallow lagoon. Once there, the animals were probably unable to

return to their normal depth. Although they concealed themselves in a rock crevice, it was only a matter of time before a predator (or collector) caught them, or death otherwise intervened.

Drifted shells of newly hatched *Nautilus* have been reported from several localities. In Fiji, four such shells were collected off Vanua Levu (Davis & Mohorter, 1973). Two of these for which there are data range from 22 to 24 mm in diameter (Davis & Mohorter, 1973:pl. 1, fig. 7, table 1). One has seven septa without septal approximation, and the other has eight septa with septal approximation between the last two septa. Both specimens lack the nepionic constriction, indicating no growth of the outer shell after hatching. Arnold et al. (1987:398) also commented on the occurrence of such shells, one of which, from the Philippines, is illustrated in Figures 2E–G. It is probable that all of these drifted individuals hatched at depths of 100–200 m, depending on the location, and were subsequently transported, possibly by currents, up the reef slope where they became stranded and died.

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Geologic and Molluscan Evidence for a Previously Misunderstood Late Pleistocene, Cool Water, Open Coast Terrace at Newport Bay, Southern California

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Abstract. A macro-invertebrate fauna from a 7 m elevation terrace remnant on the front of the Newport Mesa contains 63 mollusks, 58 specifically identified. These taxa represent a mixed death assemblage similar to that seen on rocky terrace platforms at intertidal depths in southern to central California today. The extralimital northern bivalve *Macoma inquinata* (Carpenter) and gastropods *Tectura* sp., cf. *T. persona* (Rathke), and *Tegula montereyi* (Kiener) suggest slightly cooler water temperatures than present today. These extralimital cool-water taxa, along with the terrace's geomorphic position in the palisades along the front of Newport Mesa, below other mapped terraces, separate it from the well known first terrace and its associated warm-water fauna recognized by previous authors, and suggest a younger age than the first terrace around Newport Bay.

INTRODUCTION

A poorly exposed terrace platform remnant and shoreline angle are preserved at an elevation of about 7 m above sea level in the sea cliffs along the Pacific Coast Highway, north of Newport Bay, Orange County, California (Figure 1). This paper describes the terrace remnant and its fauna, which is distinct from previously reported late Pleistocene faunas around Newport Bay.

The molluscan fauna reported here differs from the well known faunas on the higher, more extensive “first” terrace around Newport Bay (Bruff, 1946; Kanakoff & Emerson, 1959; Peska, 1975, 1976; Mount, 1981), by containing taxa that now live in cooler water than present locally today. This is unlike the fauna from the first terrace, which contains taxa suggesting water temperatures the same or warmer than exist currently along the Orange County coast.

Some specimens examined for this study were collected by the author and are housed in the Geology Department, University of California, Riverside. In addition, specimens from Bruff’s collection (housed at the Museum of Paleontology, University of California, Berkeley), and specimens from the Watts collection (housed at the Department of Invertebrate Zoology and Geology, California Academy of Sciences) were also examined.

The following abbreviations are used here: CAS—California Academy of Sciences, Department of Invertebrate Zoology and Geology; UCMP—University of California, Berkeley, Museum of Paleontology; UCR—University of California, Riverside.

PREVIOUS STUDIES

Fossil mollusks have been collected from the Newport Bay area for over 100 years (Watts, 1900; Arnold, 1903).

Both Watts (1900) and Arnold (1903) referred to fossils that probably came from the terrace remnant discussed here. Watts (1900:61) referred to fossils from “... one mile north of Newport ...” in “... dry oil-sand 2' in thickness ... interbedded with the shale,” and later (p. 223) listed 14 taxa referred from two localities from “upper oil-sand and sandstone ... West side of inner bay, Newport, Orange County.” These collections are likely to have come from the terrace remnant discussed here because of the tar-impregnation of the fossils, which occurs from this terrace remnant and have not been observed or reported elsewhere in the Newport Bay area. Also Watts (1900) showed oil-sand exposed only in the vicinity of the terrace remnant discussed here. Arnold (1903) listed 21 molluscan taxa from two localities at Newport, citing Watts (1900), one of whose localities is here referred to the terrace remnant. Later, Bruff (1946) produced a detailed account of the Pleistocene geology and fossil mollusks at Newport Bay. He listed 162 species from 12 localities around the bay. Bruff’s (1946) locality, UCMP A-3132, is on the terrace remnant, but was not recognized as distinct from other faunas around the bay. Hoskins (1957) reported fossil mollusks from three localities at Newport Bay, but all these localities are from the higher first terrace of Vedder et al. (1957) and contain extralimital warm-water taxa. By far, the most detailed work on late Pleistocene faunas around Newport Bay is that of Kanakoff & Emerson (1959) who listed nearly 500 invertebrate taxa from three localities, all from the first terrace around Newport Bay; all three of Kanakoff & Emerson’s (1959) sites contain extralimital warm water taxa. Peska (1975) and Mount (1981) described an extensive fauna from the first terrace from a road cut on the south-

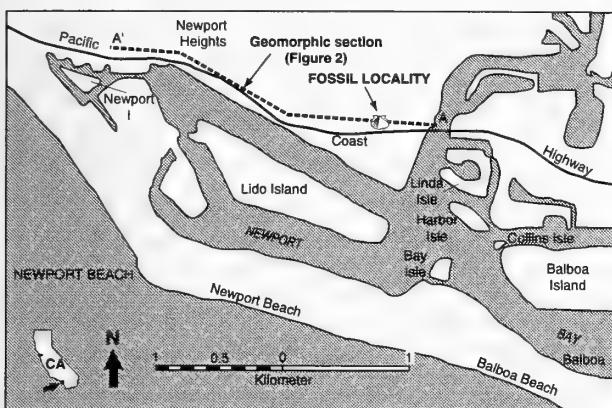


Figure 1. Index map showing location of fossil locality on terrace remnant along the palisades of Newport Mesa in Newport Heights, Orange County, California.

west extension of the Newport Freeway on the north side of Newport Mesa. This fauna contains extralimital warm-water faunal elements, including the gastropods *Eupleura muriciformis* (Broderip, 1833), *Pterynotus leeanus* (Dall, 1890), and the bivalves *Anadara perlabiata* (Grant & Gale, 1931), *Chione gnidia* (Broderip & Sowerby, 1829), and *Trachycardium panamense* (Sowerby, 1833) [as *T. procerum* (Sowerby, 1833)], among others. Peska (1976) described a similar paleoenvironment with pholad clams boring into a hard bedrock and terrace sediments overlying these deposits attributed to the first terrace because of extralimital southern molluscan taxa.

GEOLOGY AND STRATIGRAPHY

Geomorphically the terrace remnant is located on the front of the palisades that make up Newport Mesa below the top of the bluff which has been mapped as the first

terrace by Vedder et al. (1957) (Figure 2). The shoreline angle of the terrace remnant discussed here is present though not observable. This conclusion is based on the outcrop pattern of the Miocene Monterey Formation both below and above the terrace platform. Faulting of the terrace remnant into place from the higher terrace is not feasible because it would not fit the outcrop picture of the Monterey Formation (Figure 2) and there is no evidence for faulting along the front of the bluffs. Sediments making up the terrace deposits are up to 70 cm thick and are composed of a chaotic mixture of small (2–10 cm), rounded, gneissic cobbles; coarse- to fine-grained, poorly sorted, quartz-rich sand, mollusk fragments, and boulders of Monterey Formation diatomite up to 50 cm in diameter. Infaunal bivalves, including *Platyodon cancellatus* (Conrad, 1837) and pholads bored the Monterey Formation boulders and upper surface of the Monterey platform. Tar then seeped onto the terrace platform from clastic dikes in the Monterey Formation, preserving the terrace platform and immediately overlying sediments. The tar that preserved this terrace remnant originated in the underlying Monterey Formation as shown by heavy mineral analysis by Meek (1928). The geologic relationship of the terrace platform with underlying and overlying sediments is illustrated in Figure 3.

The terrace platform sediments are overlain by 1.5 to 2.5 m of fine-grained, moderately well sorted, cross-bedded, oil-impregnated sand. Because these sediments lack fossils and are moderately well sorted and cross bedded, they are believed to be eolian sands. Above and presumably behind the dune sands is Monterey Formation diatomite, which suggests that the shoreline angle is within a few meters of the terrace platform, and would be expressed in the bluff face, if exposures existed.

Fossil collections from the Newport Bay area referred to the outer Newport Bay terrace remnant reported here

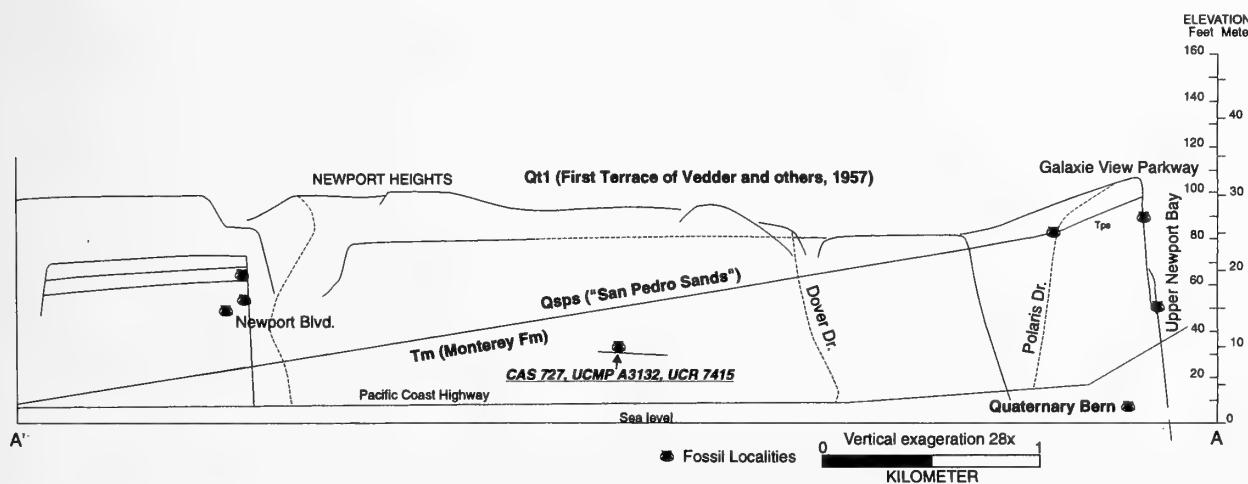


Figure 2. Geomorphic section along the front of the Newport Mesa (S. 76°E), along the Pacific Coast Highway, showing relationship of the first terrace of Vedder et al. (1957), the terrace remnant and fossil locality discussed here, and the Monterey Formation.

Table 1

Pleistocene molluscan taxa from the remnant marine terrace deposit, Newport Bay, Newport Heights, Orange County, Southern California. () = fragments.

Taxa/Localities	UCR 7415	UCMP A3132	CAS 727
Mollusca			
Bivalvia			
<i>Adula diegensis</i> (Dall, 1901)	—	2	—
<i>Chlamys</i> sp., cf. <i>C. hastata</i> (Sowerby, 1842)	(5)	1	1
<i>Crassadoma gigantea</i> (Gray, 1825)	(3)	1	—
<i>Cumingia californica</i> Conrad, 1837	13	1	—
<i>Diplodonta orbella</i> (Gould, 1851)	4	1	2
<i>Glans carpenteri</i> (Lamy, 1922)	3	1	—
<i>Kellia suborbicularis</i> (Montagu, 1803)	2	—	—
<i>Leptopecten latiauratus</i> (Conrad, 1837)	1(3)	1	—
<i>Lucinisa nuttallii</i> (Conrad, 1837)	3	—	—
<i>Macoma inquinata</i> (Carpenter, 1864)	1	1	—
<i>M. nasuta</i> (Conrad, 1837)	1(1)	—	—
<i>Mactromeris catilliformis</i> (Conrad, 1837)	1	—	—
<i>Modiolus capax</i> (Conrad, 1837)	1 (1)	—	—
<i>Mytilus californicus</i> Conrad, 1837	—	1	1 as sp.
<i>Ostrea conchaphila</i> (Carpenter, 1857)	1	2	—
<i>Parapholas californica</i> Conrad, 1837	3(2)	3	—
<i>Parvilucina</i> sp. indet.	2	—	1
<i>Penitella penita</i> (Conrad, 1837)	5	3	—
<i>Petricola californiensis</i>	3	—	—
<i>P. carditoides</i> (Conrad, 1837)	4	—	—
<i>Platyodon cancellatus</i> (Conrad, 1837)	21	5(10)	3(7)
<i>Pododesmus cepio</i> (Gray, 1850)	1	—	—
<i>Protothaca staminea</i> (Conrad, 1837)	11	7	1(4)
<i>Saxidomus nuttallii</i> Conrad, 1837	1	—	—
<i>Solen?</i> sp. indet.	2	—	—
<i>Tagelus californianus</i> (Conrad, 1837)	—	2	—
<i>Tivela stultorum</i> (Mawe, 1823)	1	—	—
<i>Trachycardium quadrangulum</i> (Conrad, 1837)	(1)	—	—
Gastropoda			
<i>Acanthina spirata</i> (Blainville, 1832)	1	—	—
<i>Agathotoma densilineata</i> Dall, 1921	—	1	—
<i>Alia carinata</i> (Hinds, 1844)	3	8	—
<i>Amphissa versicolor</i> Dall, 1871	3(1)	2	—
<i>Astyris gausapata</i> (Gould, 1850)	—	7	—
<i>Calliostoma canaliculatum</i> (Lightfoot, 1786)	4	2	—
<i>C. ligatum</i> (Gould, 1849)	1(2)	—	—
<i>Conus californicus</i> Reeve, 1844	3	—	—
<i>Crepidula adunca</i> Sowerby, 1825	5	3	1
<i>C. onyx</i> Sowerby, 1824	2	—	—
<i>Crepidatella dorsata</i> (Broderip, 1843)	4	1	—
<i>Diodora aspera</i> (Rathke, 1833)	1	—	—
<i>Discuria insessa</i> (Hinds, 1842)	1	—	—
<i>Fusinus kobelti</i> (Dall, 1877)	4(1)	—	—
<i>Haliotis fulgens</i> Philippi, 1945	3(11)	—	—
<i>Lacuna unifasciata</i> Carpenter, 1857	—	1	—
<i>Lirobittium</i> sp. indet.	—	2	1
<i>Maxwellia gemma</i> (Sowerby, 1879)	(1)	—	—
<i>Mitra idae</i> Melville, 1893	1	—	—
<i>Nassarius</i> sp., cf. <i>N. cerritensis</i> (Arnold, 1903)	(1)	—	—
<i>N. fossatus</i> (Gould, 1849)	3	3	4
<i>N. mendicus</i> (Gould, 1849)	4	—	—
<i>N. perpinguis</i> (Hinds, 1844)	2	1	3
<i>Neverita reclusiana</i> (Deshayes, 1839)	2(1)	—	—
<i>Ocenebra</i> sp. indet.	(1)	—	—
<i>Odostomia</i> sp. indet.	2	2	—

Table 1
(Continued)

Taxa Localities	UCR 7415	UCMP A3132	CAS 727
<i>Olivella biplicata</i> (Sowerby, 1825)	30	10	—
<i>O. baetica</i> Carpenter, 1864	2	2	—
<i>Pseudomelatoma torosa</i> (Carpenter, 1865)	1(1)	—	—
<i>Serpulorbis squamigerus</i> (Carpenter, 1857)	7	1	—
<i>Tectura</i> sp., cf. <i>T. persona</i> (Rathke, 1833)	1	—	—
<i>Tegula montereyi</i> (Kiermer, 1850)			
Polypolacophora			
<i>Callistochiton</i> sp. indet.	1	—	—
Scaphopoda			
<i>Dentalium neohexagonum</i> Pilsbry & Sharp, 1897	1	—	—

include a collection by W. S. Watts from the old State Mining Bureau collections, now housed at the California Academy of Sciences; University of California Museum of Paleontology locality A-3132 reported by Bruff (1946); and collections from UCR 7415. Watts' locality data is confusing and cannot be exactly placed, but the tar impregnating the fossils (and sediments) in his collection is distinctive and has not been reported (or observed) elsewhere in the Newport Bay area, and the map in Watts (1900) locates his collections in approximately the same locality studied here. Watts' collection does not add any taxa not also reported by Bruff (1946) and herein. Bruff's (1946) collection can be located fairly well as the terrace remnant discussed here in part because the fossils are all tar impregnated, suggesting that they came from the same locality.

PALEOECOLOGY

The fauna from the outer Newport Bay terrace remnant (Table 1) consists of 64 molluscan taxa (32 gastropods, 30 bivalves, one scaphopod, and one chiton). These taxa represent a mixed death assemblage similar to that found on intertidal rocky platforms in Southern California today. In situ taxa represent the exposed rocky shore *Mytilus californianus*-*Littorina planaxis* community of Valentine (1961) and include the gastropods *Haliotis fulgens*, *Acanthina spirata*, *Tectura persona* (questionably identified here), *Diodora aspera*, and the bivalves *Cumingia californica*, *Penitella penita*, *P. gabbii*, and *Parapholas californica*. Valentine's (1961) cold water *Tegula brunnea* (Philippi, 1848) element is represented by the extralimital occurrence of *Tegula montereyi* and *Macoma inquinata*. Other taxa from this mixed death assemblage represent several nearby environments, including kelp forest (e.g., *Calliostoma cancellatum*, *Discurria insessa*, *Mitra idae*, *Tegula montereyi*, and *Leptopecten latiauratus*) and a sandy environment (e.g., *Conus californicus* Reeve, *Nassarius* spp., *Olivella* spp., *Neverita reclusianus*, *Epilucina californica*, and *Macoma nasuta*). The abundant occur-

rence of *Olivella biplicata* in this fauna would normally suggest a protected sandy environment (Onuf, 1972), but Valentine (1980) showed that hermit crabs concentrate these shells on rocky terrace platforms.

The molluscan taxa reported here show a maximum overlap of latitudinal range zones at about 34°N, or slightly north of the latitude of the fossil locality (33°N) (Figure 4). Extralimital northern taxa with southern endpoints slightly to the north of the fossil locality include: *Macoma inquinata*, with a modern range from the northern Bering Sea, Alaska south to San Pedro, Los Angeles County, California (Coan, 1971); *Tegula montereyi*, which occurs in California from Bolinas Bay south to Santa Barbara Island off the Santa Barbara coast (Abbott, 1974); and *Tectura persona*, which occurs from the Shumagin Islands, Alaska to Morro Bay, central California (Lindberg, 1981). *Chlamys hastata* (questionably identified here) (Bernard, 1983) and *Calliostoma canaliculatum* (Burch, 1944–1946) have their southern endpoints within one degree of the fossil locality (between 32°N and 34°N). There is one questionably identified southern extralimital taxa. A fragment of a body whorl questionably identified as *Nassarius cerritensis* is present in the collection from UCR 7415. Keen (1971) cited a range for *Nassarius cerritensis* (questionably identified here) including the outer coast of Baja California. Examination of collections at the Los Angeles County Museum of Natural History and the California Academy of Sciences confirms a northern range limit of 30°N. These data, with the exception of *Nassarius cerritensis*, suggest that temperatures may have been slightly cooler during deposition of this terrace platform than exist along the Orange County coast today.

The paleobathymetry determined here, using overlapping depth range data (Figure 5) from living representatives (Bernard, 1983, for the Bivalvia and various sources for the Gastropoda) of the terrace fauna, indicates that deposition occurred between the intertidal zone and about 5 m. Only *Epilucina californica* (30–75 m) and *Luciniscia nuttalli* (10–75 m) are reported from deeper water depths

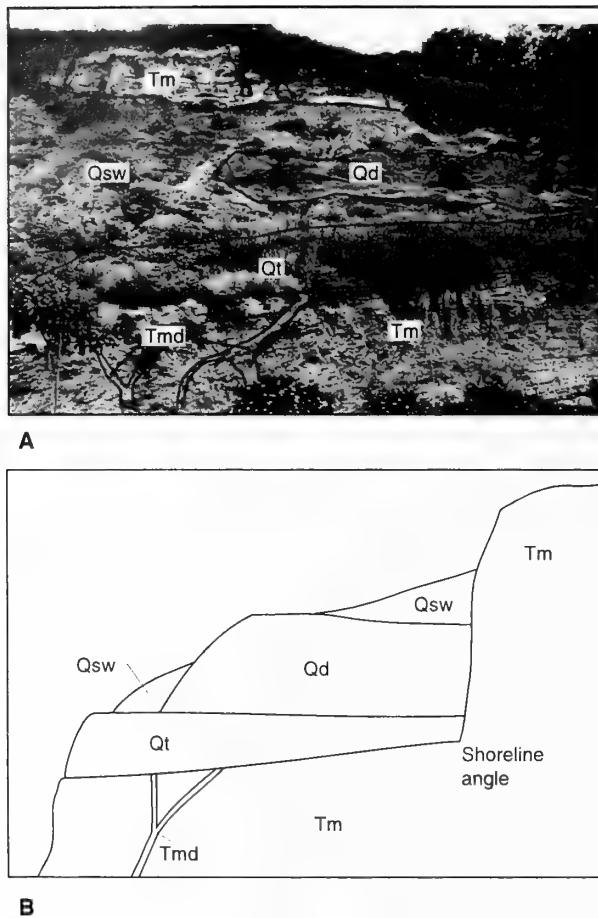


Figure 3. A. View of the outcrop in 1977; it has since become overgrown with vegetation. Note the Monterey Formation outcropping both below the terrace deposit and above the dune sand and slope wash at the back of the terrace platform. Tm = Tertiary, Monterey Formation; Tmd = Tertiary, Monterey Formation, dike; Qt = Quaternary, terrace deposit; Qd = Quaternary, dune sand; Qsw = Quaternary slope wash. B. Geomorphic cross section showing interpretation of beds observed in outcrop and location of inferred shoreline angle. This illustration is approximately 90° along a vertical axis from Figure 3A.

(Bernard, 1983) in the modern fauna. It is interesting to note that even though the modern depth range of *E. californica*, and to a lesser extent *L. nuttalli*, is outside the intertidal to shallow subtidal depth zone suggested by the rest of the fauna, they are very common constituents of open coast, modern and late Pleistocene terrace platform faunas in Southern California, which otherwise represent intertidal to shallow subtidal depths, and both can be found dead at intertidal depths.

AGE AND CORRELATION

No numerical age determinations have been performed from this terrace remnant. The fauna from the terrace remnant is thought to correlate with the early part of ox-

ygen isotope stage 5 (5a or 5c) (of Shackleton & Opdyke, 1973) because of the cool water extrazonal taxa present. Similar cool water faunas reported from the San Pedro area have been correlated with stage 5a and 5c using amino-acid racemization, geomorphic data, and temperature aspects of the fauna (Lajoie et al., 1991; Ponti, 1989; Ponti et al., 1991; unpublished data).

Ongoing research indicates molluscan faunas from older deposits (oxygen-isotope stages 5e, 7, and 9) suggesting warmer water conditions than present along the adjacent coast because of the occurrence of extrazonal southern taxa (Powell, unpublished data). It is possible that the fauna here is older than early stage 5 and was subjected to upwelling along the open coast, resulting in a cooler than normal fauna. This may be suggested by the occurrence of *Nassarius cerritensis* in the UCR collection. However, this specimen is represented by a single fragment that is questionably identified (cf.), so it may not be this extrazonal taxon or could have been reworked from older Pleistocene deposits around Newport Bay. In either case, it is discounted in interpretations of the paleoenvironment. An age older than stage 9 can be generally ruled out because deposits of this age are generally found at much greater altitudes (see Barrie et al., 1992), and commonly contain extinct taxa (Powell et al., 2000).

Deposits younger than oxygen-isotope stage 5 have not been recognized onshore in the greater Los Angeles Basin, but have been recognized in the Ventura Basin (Lajoie et al., 1982; Yerkes et al., 1987), so their occurrence in the Newport area is possible, though unlikely. Assuming the first terrace represents the stage 5e highstand, as generally accepted (Kennedy et al., 1982), and the terrace remnant represents stage 3, then that would argue for an increase in uplift rates in the last 60 ka than suggested by the first terrace and the nearby San Joaquin Hills (Grant et al., 1999). I do not favor this for the following reasons: (1) based on molluscan faunas from dated sea-level highstands and lowstands, I would expect mollusks from stage 3 deposits to represent cooler water temperatures than suggested here; and (2) uplift rates in the general area as shown by Grant et al. (1999) and Barrie et al. (1992) are not high enough to bring stage 3 deposits above sea level, much less younger deposits. Mollusks from lowstand deposits attributed to oxygen isotope stage 2 have been recognized elsewhere in California (Powell et al., 1992; Powell, 1994) but are found at a depth greater than 100 m, and the biogeographic character of the fauna is much cooler than present. Faunas younger than oxygen-isotope stage 2 are essentially modern in biogeographic character and are found at deep to shallow water depths in the ocean (Powell et al., 1992; Powell et al., 2000).

If the fauna correlates to early oxygen-isotope stage 5 as suggested here, then it most likely was deposited be-

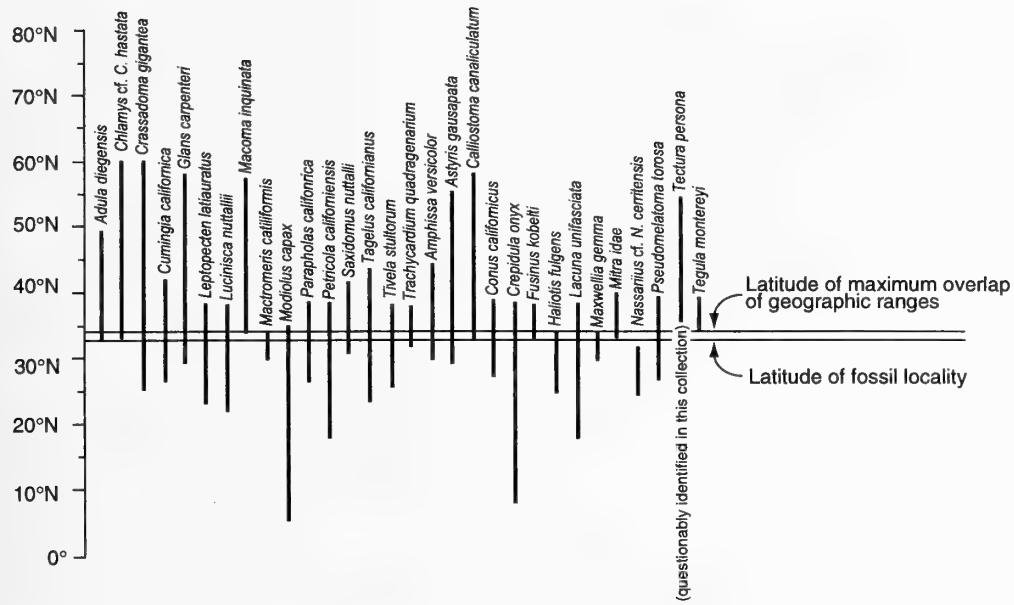


Figure 4. Latitudinal distribution of selected mollusks recovered from the terrace deposit. Data from Bernard (1983), Dall (1921), Keen (1937), Keen (1971), Lindberg (1981, 1988), Marinovich (1977), McLean (1966, 1983), McLean & Gosliner (1996), Morris et al. (1980), and museum collections. The lower line indicates the latitude of the fossil locality. The upper line shows the zone of maximum overlap of mollusk distributions at 34°N, or slightly north of the latitude at which the fossils were collected.

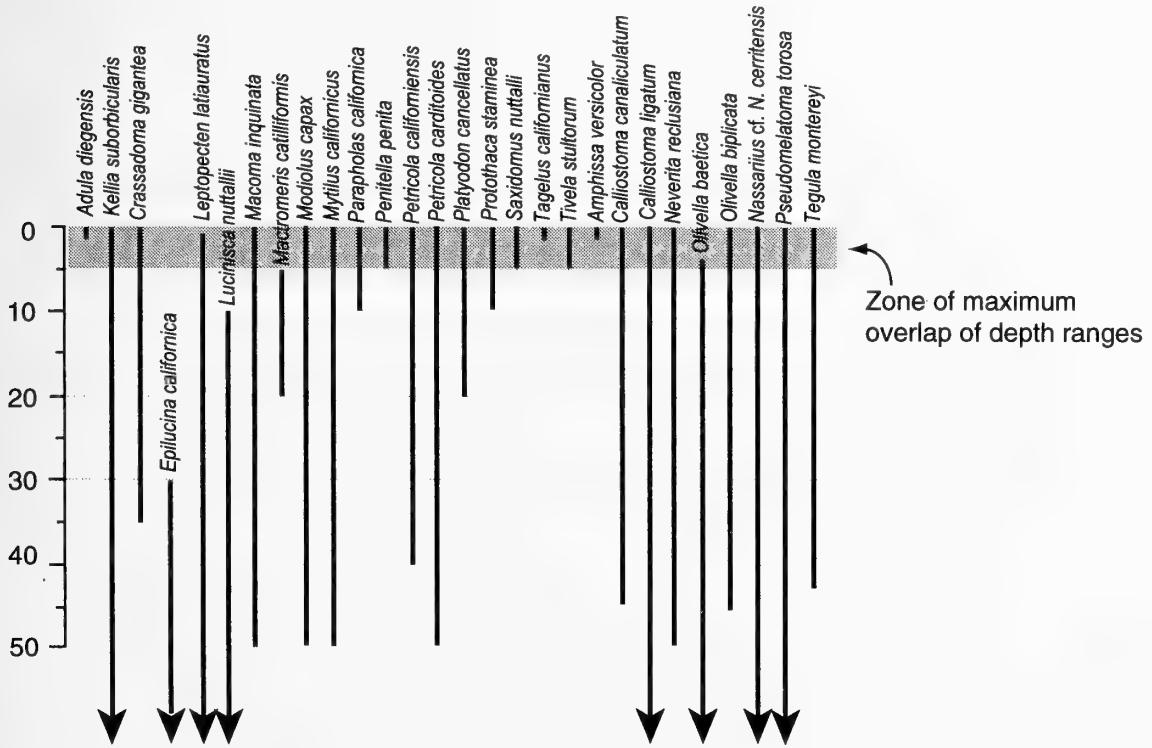


Figure 5. Depth distribution of selected mollusks recovered from the terrace deposit. Data from Bernard (1983), Burch (1944–1946), Groves (1991), Marinovich (1977), McLean & Gosliner (1996), Scott (1998), and museum collections. This figure shows maximum overlap of distributions between the intertidal zone and 5 m, with only *Epilucina californica* (30–75 m) and *Lucinisa nuttalli* (10–75 m) occurring outside that range.

tween 105 ka and 85 ka (Chappell, 1983; Chappell & Shackleton, 1986).

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APPENDIX: LOCALITY DATA

California Academy of Sciences, San Francisco

CAS 727: “Fossil shells from west side of Inner Bay, Newport, Orange County, California. Upper oil sand and sandstone. W. S. Watts collections #9 and #10. From State Mining Bureau Collections. Pliocene.”

University of California, Berkeley, Museum of Paleontology

UCB A-3132: Cross-bedded sand with conglomerated saturated oil and fossil fragments. Along face of pali-sades 1 map inch due south of “S” in Newport Heights, 3.5” due west of bench mark on top of pali-sades just above “A” in coast along Pacific Coast Highway. SW1/4, NW1/4, SW1/4, section 27, Newport Beach Quadrangle. Collected by W. Bruff, December 1938.

University of California, Riverside, Department of Geology

UCR 7415: Terrace remnant about 7 m above sea level and extends south for about 160 m, located in bluff behind business and parking lot at 1400 Pacific Coast Highway, Newport Heights, Newport Beach, Orange County, California. $37^{\circ}31'N$, $118^{\circ}24'15"W$. Collected by C. Powell, II, 1971–1978.

Eastern Pacific Species of the Venerid Genus *Cyclinella* (Bivalvia)

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Abstract. In spite of the number of available names, there are only three eastern Pacific species of *Cyclinella*. (1) *Cyclinella jadisi* Olsson, 1961, occurs from the head of the Gulf of California to Guayas Province, Ecuador, from the intertidal zone to 31 m. (2) *Cyclinella producta* (Carpenter, 1856) occurs from Laguna Ojo de Liebre, Pacific coast of Baja California Sur, throughout the Gulf of California, to Tumbes Province, Peru, on intertidal mudflats; *C. singleyi* Dall, 1902, is a synonym. (3) *Cyclinella subquadrata* (Hanley, 1844) occurs from Isla Cedros, Pacific coast of Baja California, throughout the Gulf of California, to Lima Province, Peru, from the intertidal zone to 75 m. *Venus kroeyeri* Philippi, 1847; *Artemis macilenta* Reeve, 1850; *Arthemis saccata* Gould, 1851; *Cyclinella galera* Pilsbry & Olsson, 1941; and *C. kroeyeri ulloana* Hertlein & Strong, 1948, are regarded as synonyms of *C. subquadrata*. Other Recent taxa that have been referred to *Cyclinella* are discussed, and those from the fossil record are listed.

INTRODUCTION

Panamic province members of the venerid genus *Cyclinella* have been a particular puzzle. Olsson (1961) described one new species, *C. jadisi*, and listed four others—*C. subquadrata* from northwestern South America, *C. saccata* from the Gulf of California to Panama, *C. ulloana* from the Gulf of California, and *C. singleyi* from the Gulf of California to Peru. Keen (1971) listed *Cyclina producta* Carpenter from Panama as a *Cyclinella*, along with the same five taxa as Olsson. She also mentioned *C. kroeyeri*, occurring from Peru to Chile, beyond the southern limit of her book, bringing the number of species to seven. In his checklist, Bernard (1983) also listed these seven.

Previous reviews that include species of *Cyclinella* are those of Reeve (1850), Sowerby (1852), Dall (1902b, 1903), Palmer (1927–1929), Hertlein & Strong (1948), Keen (1958), Olsson (1961), Keen (1971), and Fischer-Piette & Vukadinovic (1972). The characters given by Hertlein & Strong (1948), Olsson (1961), and Keen (1971) for differentiating the taxa of the genus, and the information on the distributions of eastern Pacific species, are inaccurate and contradictory.

The purposes of the present study were to assess the correct identity of the species of *Cyclinella* inhabiting the eastern Pacific and to accurately document their differentiating characters and distributions.

FORMAT

In the following treatment, each valid taxon is followed by a synonymy, information on type material and type localities, notes on distribution and habitat, and additional discussion.

The synonymies include all major accounts about the species, but not most minor mentions in the literature. The entries are arranged in chronological order under each species name, with changes in generic allocation from the previous entry, if any, and other notes given in parentheses.

The distributional information is based on Recent specimens I have examined. Fossil occurrences are taken from the literature.

References are provided in the Literature Cited for all works and taxa mentioned.

The following abbreviations for institutions are used in the text: BM(NH), British Museum (Natural History) collection, The Natural History Museum, London, England; CAS, California Academy of Sciences, San Francisco, California, USA; LACM, Natural History Museum of Los Angeles County, California, USA; USNM, United States National Museum collection, National Museum of Natural History, Smithsonian Institution, Washington, DC, USA; UMML, University of Miami Marine Laboratory, Rosenstiel School of Marine and Atmospheric Sciences, Miami, Florida, USA; Skoglund Collection, collection of Carol Skoglund, Phoenix, Arizona, USA.

MORPHOLOGICAL CHARACTERS

In their key to *Cyclinella*, Hertlein & Strong (1948:179) used inflation and the more vertically directed pallial sinus to separate *C. singleyi* (here *C. producta*) from other species, as well as lunule shape, which I do not find di-

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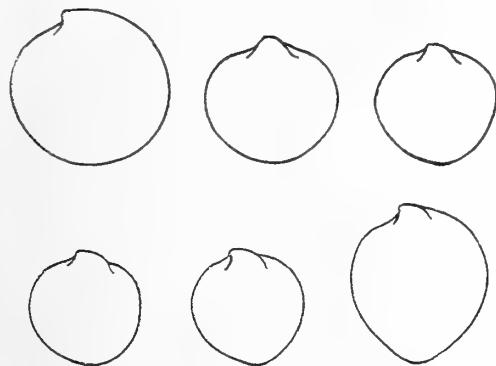


Figure 1. Copy of Fischer-Piette & Vukadinovic's (1972) figure 4, showing the variability in outline of *Cyclinella tenuis*.

agnostic. Subsequent couplets in their key used variable shape characters and non-diagnostic aspects of pallial sinus form. In his key to the genus, Olsson (1961:262) used maximum size as the first couplet to separate *C. singleyi* from everything else. While true, this is a useless character for small specimens. In his second couplet, variable, subjective shape characters were used.

Some aspects of shell shape are of some importance in differentiating the three species. Fischer-Piette & Vukadinovic (1972) showed that the Caribbean *C. tenuis* has a significantly variable outline (Figure 1, a copy of their fig. 4). While *C. subquadrata* has a similarly variable outline, the other two eastern Pacific taxa are much less plastic, and differ in specific ways from *C. subquadrata* in spite of its variability. The most important shape character proves to be the degree of inflation of the shell and of the beaks. Shell sculpture and the distinctness of the lunule are not useful characters, in spite of their mention in some species descriptions. Shell color is characteristic of one taxon. The hinge does not provide many significant

cant characters, most elements varying within each species in similar ways; the direction of the posterior cardinal teeth is minimally helpful. Internally, the direction of the pallial sinus (defined by a line bisecting it) and the partially discontinuous anterior leg of the pallial sinus are distinct in one taxon. The position of the posterior adductor muscle scar relative to the hinge plate also differs among the species. The size measurements made are shown in Figure 2. The most important differentiating characters are given in Table 1.

TAXONOMIC DISCUSSION

Cyclinella Dall, 1902

Cyclinella Dall, 1902a:44. Type species (subsequent designation: Dall, 1902b:357): *Dosinia (Artemis) tenuis* Récluz, 1852:250–252. Recent, western Atlantic.

Shell ovate; length generally equal to or slightly greater than height. Sculpture of fine commarginal striae. Lunule evident, weakly outlined; escutcheon absent. Pallial sinus short to moderate length, of medium width, and directed toward beaks, toward anterior adductor muscle scar, or between them. Three cardinal teeth in each valve; no lateral teeth; anterior cardinals thin; central cardinals of medium width to broad; posterior cardinals of medium width to thin, elongate, that in right valve bifid. With a deep pit of variable size on hinge plate near anterior end of ligament.

The type species of this genus has generally been regarded as having been established by original designation (as, for example, Keen, 1969:681). However, the wording in Dall (1902a:44) is ambiguous at best, and he included three species in the genus: *C. tenuis* (Récluz, 1852), *C. subquadrata* (Hanley, 1844), and his new *C. singleyi*. The type species was established as being the first of these only by the subsequent designation in Dall (1902b:357).

Table 1.

Key differentiating characters, size, and frequency of eastern Pacific *Cyclinella*

	Inflation	Anterior leg of pallial line	Beaks/Umbones	Pallial sinus points	Posterior adductor scar position	Maximum size, mm	No. of eastern Pacific lots studied
<i>C. jadisi</i>	Flattened, l/w = 2.3–2.7	Continuous (with smaller dorsal scars)	Low, purplish brown	Between anterior adductor and umbones	Close to hinge plate	70.1	28
<i>C. producta</i>	Inflated, l/w = 1.5–1.7	Discontinuous scars	Inflated, white	Toward umbones	More distant from hinge plate	43.3	70
<i>C. subquadrata</i>	Moderately inflated, l/w = 1.9–2.3	Continuous (with smaller dorsal scars)	Moderately inflated, white	Between anterior adductor and umbones	More distant from hinge plate	81.3	169
							Total lots: 267

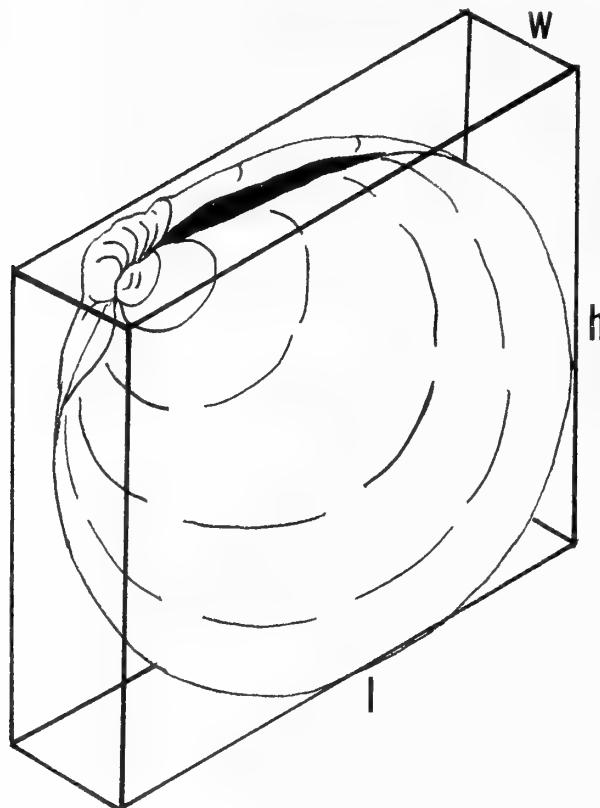


Figure 2. Positions of measurements made of *Cyclinella*—length (l), height (h), and width (w).

This genus, thus far known only from the Americas, is most similar to *Dosinia* Scopoli, 1777:399, differing from it in having thinner shells, lacking a lateral tooth in the left valve, and having less pronounced commarginal sculpture. Unlike some species of *Dosinia*, the lunule is shallow, and there is no escutcheon. *Cyclinella* is similar to *Dosinia* in having an oval shell, and the pallial sinuses of many species of *Dosinia* are also anterodorsally directed (Fischer-Piette & Delmas, 1967: for example, their pls. 13–15).

Several nominal species of *Cyclinella*, as well as many species of *Dosinia*, were originally proposed in *Artemis* Conrad, 1832:20, a widely used misspelling of *Arthemis* Poli, 1791:252, 258, which is an objective synonym of the subgenus *Dosinia* (*Pectunculus*) da Costa, 1778:183 (Keen, 1969:680). (*Artemis* is also non Kirby & Spence, 1828, vol. 3:248, a butterfly genus.)

Because species of *Cyclinella* have relatively thin shells, they require care in handling and packing. Many museum specimens have been cracked or broken by careless handling.

The anatomy of the western Atlantic *Dosinia concentrica* (Born, 1778:58) was investigated by Castro Guérón & Santos Coelho (1989), who illustrated the fused siphons of this species (their figs. 8, 9, p. 19). From dried

animals in three eastern Pacific lots of *Cyclinella subquadrata*, it is apparent that this genus also has fused siphons (Skoglund Collection, Bahía San Carlos, Sonora, Mexico; Skoglund Collection, Juncalito, Baja California Sur, Mexico; CAS 117652, Bahía de los Angeles, Baja California, Mexico). Based on dried specimens of *Cyclinella*, Dall (1903:1284) described the foot as being small, pointed, and triangular.

Cyclinella has been placed in the subfamily *Cyclininae* Frizzell, 1936b:64¹ (as, for example, Keen, 1969:681). Harte (1998) demonstrated that the type genus of this subfamily, *Cyclina* Deshayes, 1850:623,² is instead more likely to belong in the *Chioninae* Frizzell, 1936b:65,¹ and she suggested that *Cyclinella* might instead belong in either the *Clementiinae* Frizzell, 1936b: 64,¹ or the *Tapetinae* Deshayes, 1853:4, 159, ex Gray ms. In contrast, I believe that a relationship to the *Dosininae* Deshayes, 1853:3, 5, ex Gray ms, is more likely. In addition to the shared characters mentioned above, *Cyclinella* and *Dosinia* share a deep pit on the hinge plate near the beaks. Dall (1902a, b) suggested a relationship of *Cyclinella* to the unique European type species of *Mysia* Lamarck, 1818:543, *M. undata* (Pennant, 1777:81 in quarto ed., p. 95 in octavo ed., pl. 55, fig. 51, as *Venus*), the anatomy of which was discussed by Ansell (1961:509–511). *Mysia* also has an orbicular shape, a thin shell, and a dorsally directed pallial sinus. However, it has long, separate siphons and only two cardinal teeth in the right valve. As a result, many authors have placed *Mysia* in the Petricolidae (for example, Keen, 1969:689). Only the addition of anatomical and biochemical characters will resolve the question of the relationships among these genera.

Cyclinella jadisi Olsson, 1961

(Figures 3, 16)

Cyclinella jadisi Olsson, 1961

Olsson, 1961:264, 516, pl. 43, fig. 2; Keen, 1971:179, 180, fig. 429; Fischer-Piette & Vukadinovic, 1972:147.

Type material and locality: ANSP 218900, holotype; length, 61.7 mm; height, 59.1 mm; width, 26.6 mm (Figure 3). UMML 30.11167, paratypes, 1 pair, 4 valves—pair, length, 67.9 mm; right valve, length, 70.1 mm; left valve, 62.5 mm; left valve, 41.3 mm; left valve, 36.6 mm. Palo Seco, Panama (9.0°N); Stewart Jadis, collector.

Description: Shell ovate, length equal to or slightly greater than height ($l/h = 1.0\text{--}1.1$; $n = 8$); anterior end rounded; posterior end rounded to subtruncate; flattened ($l/w = 2.3\text{--}2.7$; mean, 2.5; $n = 7$); beaks low, not inflated.

¹ The earlier appearance of these family-group names in a 1936 abstract (Frizzell, 1936a:415) are *nomina nuda* because there are no descriptions (ICZN Code Art. 13.1).

² The type species of *Cyclina* is *Venus sinensis* Gmelin, 1791: 3285, by the subsequent designation of Dall (1902b:348).

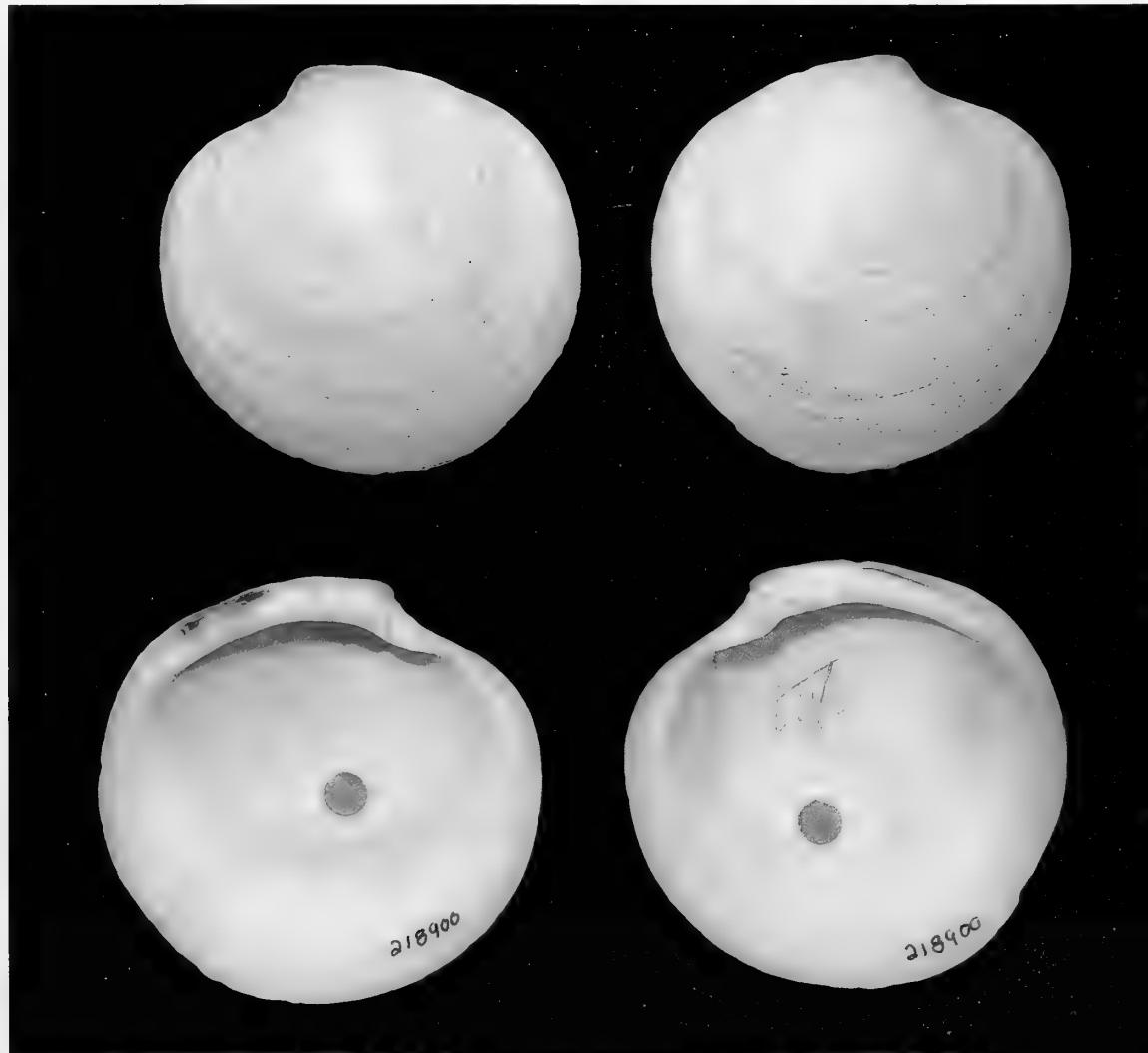


Figure 3. *Cyclinella jadisi* Olsson, 1961. Holotype of *C. jadisi*; length=61.7 mm.

Exterior surface with a thin, light tan periostracum; umbones purplish brown, rarely white. Interior white, often pinkish tan dorsally. Anterior end of pallial line continuous, with a series of smaller scars above it; pallial sinus directed to between anterior adductor muscle scar and umbones; posterior adductor muscle scar positioned closer to hinge plate than in other species (Figure 16). Posterior cardinals straight. Length to 70.1 mm (UMML 30.11167, a paratype).

Distribution and habitat: From the head of the Gulf of California at Bahía Cholla, Sonora, Mexico (31.4°N) (Skoglund Collection), south to Playas and Salitro, Guayas Province, Ecuador (2.7°S) (Skoglund Collection), from the intertidal zone to 31 m (mean 12.7 m; n = 15); the only bottom types noted on labels are sand and mud. This is the least common of the three eastern Pacific species; I have seen only 28 lots, including the types.

Discussion: This species is sympatric with the more common *Cyclinella subquadrata* throughout the Panamic province, although the two have rarely been obtained from the same station. It is most easily distinguished by its flatter shape and purple beaks.

This species seems very similar to *Cyclinella harrisi* Palmer, 1927, described from the Springvale Miocene of Trinidad, which also has a flattened form (original measurements: l = 62 mm; h = 57 mm; w = 20 mm). Only a closed pair was figured by Palmer (1927).

Cyclinella producta (Carpenter, 1856)

(Figures 4, 5, 17)

Cyclina producta Carpenter, 1856

Carpenter, 1856:161; Carpenter, 1857a:284, 305; Römer, 1860:159; Dall, 1902b:392 (*Cyclinella*); Keen, 1958:

138; Palmer, 1963:308, 394, pl. 64, figs. 10–13; Keen, 1971:179, 180, fig. 430.

Cyclinella singleyi Dall, 1902

Dall, 1902a:44; Dall, 1902b:392, 404, 411, pl. 15, fig. 3; Hoffstetter, 1952:30; Keen, 1958:138, 139, fig. 309; Olsson, 1961:264, 516, pl. 43, fig. 5, 5a; Keen, 1971: 179, 180, fig. 432; Fischer-Piette & Vukadinovic, 1972: 147.

Type materials and localities: *C. producta*—BM(NH) 19621112, holotype, pair; length, 40.4 mm; height, 40.1 mm; width, 26.7 mm (Figure 4). Panama Bay, Panama (approximately 9.0°N); Thomas Bridges, collector.

C. singleyi—USNM 108817, **lectotype** (here designated), pair; length, 39.9 mm; height, 39.3 mm; width, 24.3 mm (Figure 5). USNM 880621, paralectotype, pair; length, 36.7 mm. Delta of Río Yaqui, Sonora, Mexico (27.7°N); J.A. Singley, collector. The lectotype selected is the largest specimen and that figured by Dall (1902b).

Description: Shell subquadrate-ovate, length equal to or slightly greater than height ($l/h = 1.0\text{--}1.1$; $n = 10$); anterior end sharply rounded; posterior end subtruncate; inflated ($l/w = 1.5\text{--}1.7$; mean 1.6; $n = 10$); beaks inflated, prominent. Exterior surface of unworn specimens with a thin, tan periostracum. Interior white, sometimes with a light pink flush. Anterior end of pallial line composed of a series of mostly discontinuous scars; pallial sinus directed toward umbones. Posterior adductor muscle scar positioned well below hinge plate (Figure 17). Posterior cardinals curved ventrally. Length to 43.3 mm (ANSP 155502; La Union, El Salvador).

Distribution and habitat: Laguna Ojo de Liebre (Scammons), Pacific coast of Baja California Sur (27.8°N) (CAS 117653), into and throughout the Gulf of California, to its head at Bahía Cholla, Sonora (31.4°N) (Skoglund Collection), Mexico, south to Puerto Pizarro, Tumbes Province, Peru (3.5°S) (UMML 30.11148, 30.11158, 30.11162; LACM 72–84), and probably to Punta Picos, Tumbes Province, Peru (3.5°S) (UMML 30.1115, fragments). Aside from beach drift, all records are from intertidal zone mudflats. I have seen 70 lots, including the types.

This species has been recorded from the late Pleistocene terraces at Newport Bay, Orange County, California (LACM 62-2; Kanakoff & Emerson, 1959:22).

Discussion: It is surprising that workers have not recognized the similarity of Carpenter's *Cyclina producta* to Dall's *Cyclinella singleyi*, particularly after its holotype was illustrated by Palmer (1963).

Cyclinella subquadrata (Hanley, 1844)

(Figures 6–15, 18)

Artemis subquadatra Hanley, 1844

Hanley, 1844:11, pl. 15, fig. 39; 1856:357; Hanley, 1845: 11–12; Reeve, 1850:pl. 3, fig. 15; Sowerby, 1852:661–

662, pl. 141, fig. 27; Deshayes, 1853:31 (*Cyclina*); Carpenter, 1857b:62–63; Römer, 1860:159; Pfeiffer, 1869: 115–116, pl. 28, figs. 10–12; Dall, 1902b:391 (*Cyclinella*); Lamy, 1910:89; Bosworth, 1922:177, pl. 25, fig. 15; Hertlein & Strong, 1948:180–181; Keen, 1958:138, 139, fig. 310; Olsson, 1961:263, 528, pl. 55, fig. 2; Keen, 1971:179, 180, fig. 433; Fischer-Piette & Vukadinovic, 1972:141–146, figs. 7–12.

Venus (Artemis) kroeyeri Philippi, 1847

Philippi, 1847:87 (as "kröyeri"); Philippi, 1848:26 (= 78), pl. 7, fig. 9; Deshayes, 1853:32 (*Cyclina*); Hupé, 1854: 338; Römer, 1860:159; Pfeiffer, 1869:116–117, pl. 31, figs. 1–3; Dall, 1902b:391 (*Cyclinella*); Riveros-Zuñiga & Gonzales Reyes, 1950:124–125; Soot-Ryen, 1957:8; Keen, 1958:136, 137, fig. 307; Fischer-Piette & Vukadinovic, 1972:144, 147.

Artemis macilenta Reeve, 1850

Reeve, 1850:pl. 9, fig. 51; Sowerby, 1852:662, pl. 154, fig. 32; Deshayes, 1853:31–32 (*Cyclina*); Keen, 1971: 180 (as possibly = *Cyclinella subquadrata*).

Arthemis saccata Gould, 1851

Gould, 1851:91; Gould, 1853:396–397, pl. 15, fig. 2; Adams, 1852a:400 (1852b:275) (as "Artemis"); Deshayes, 1853:32 (*Cyclina*); Carpenter, 1857b:62 (as = *C. subquadrata*); Römer, 1860:159; Johnson, 1964:144; Olsson, 1961:263–264, 513, 515, 516, pl. 40, fig. 6; pl. 42, fig. 4, 4a; pl. 43, figs. 4, 4a, 6, 6a; Keen, 1971: 179, 180, fig. 431.

Cyclinella galera Pilsbry & Olsson, 1941

Pilsbry & Olsson, 1941:66, 78, 79, pl. 12, fig. 1, pl. 19, fig. 4.

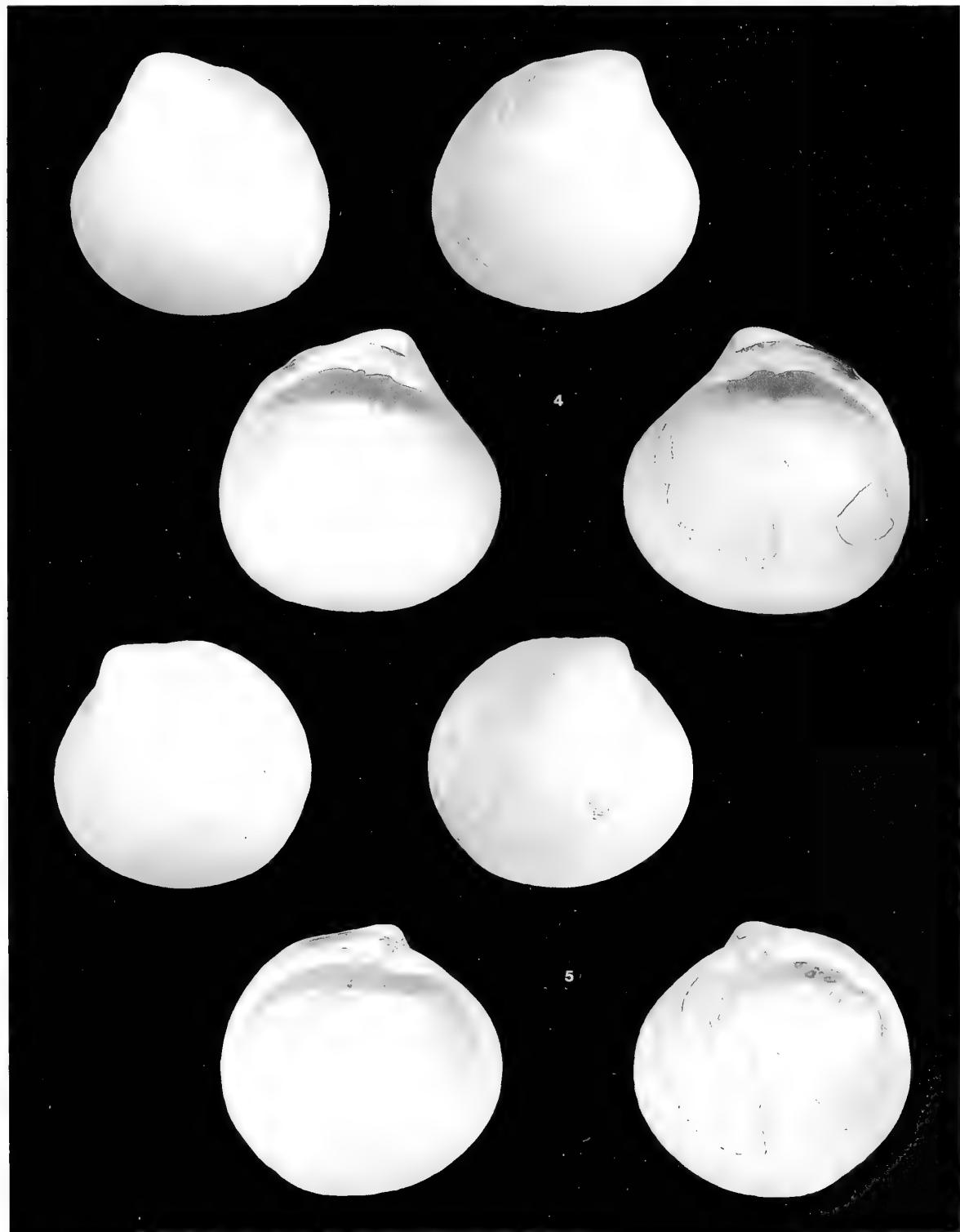
Cyclinella kroeyeri ulloana Hertlein & Strong, 1948

Hertlein & Strong, 1948:179–180, 197, pl. 2, figs. 5–7; Keen, 1958:137, fig. 307a; Olsson, 1961:264, 516, pl. 43, fig. 3; Keen, 1971:180, 181, fig. 434; Fischer-Piette & Vukadinovic, 1972:147.

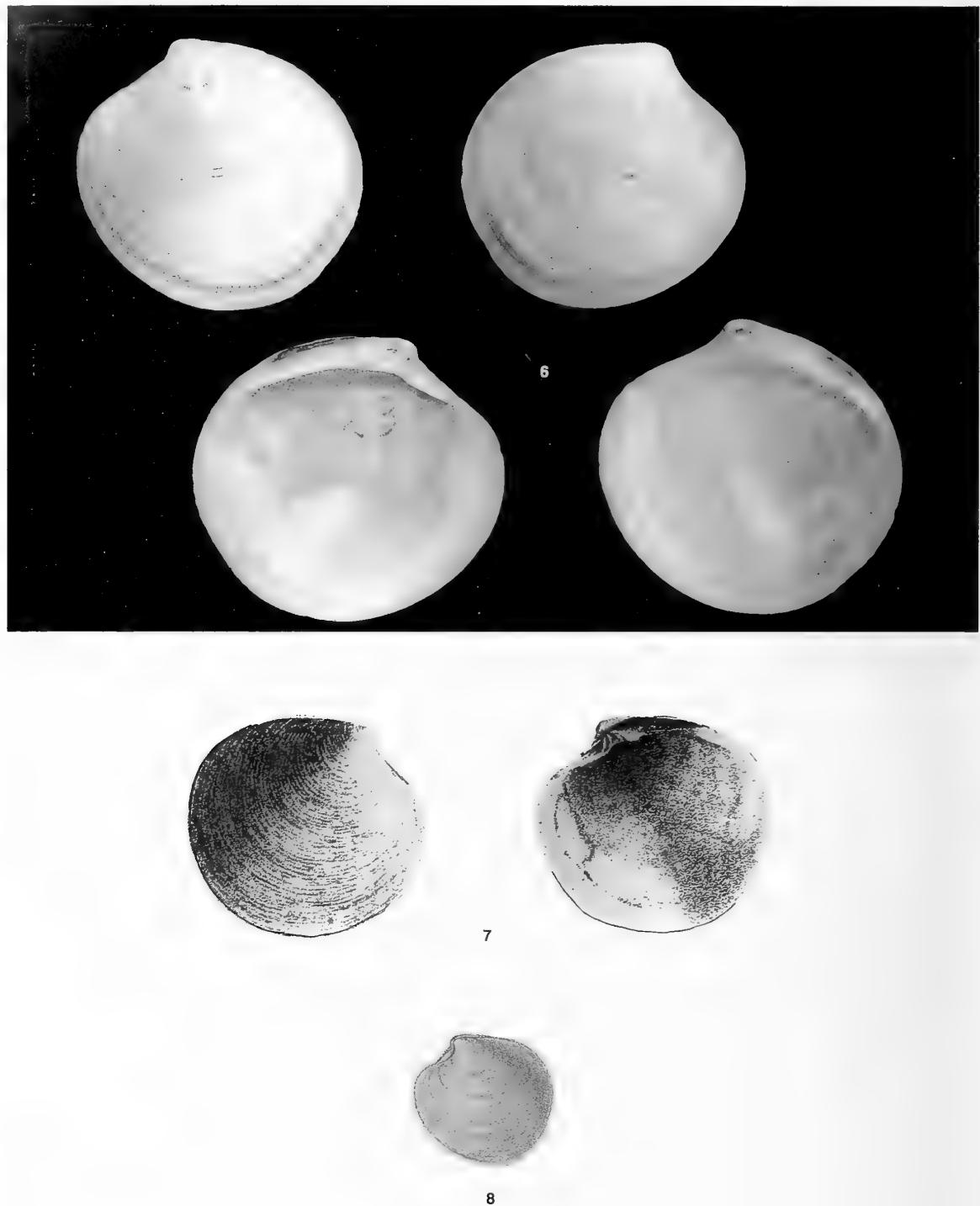
Type materials and localities: *A. subquadrata*—BMNH 1998196/1, **lectotype** (here designated); length, 35.1 mm; height, 32.1 mm; width, 16.8 mm (Figure 6). BMNH 1998196/2, paralectotype; length, 26.4 mm. Santa Elena, Guayas Province, Ecuador (2.2°S); Hugh Cuming, collector. Hanley (1845) gave a length of 44.5 mm, but this specimen has not been detected in the BMNH. The lectotype selected is the larger of the two extant type specimens.

V. (A.) kroeyeri—Lost. Not in the Museum für Naturkunde, Berlin (M. Galubrech, e-mail, 4 May 1999), nor in the Museo Nacional de Historia Natural, Santiago, Chile (D. Frassinetti, e-mail, 24 August 1999). Philippi's 1848 figure is 27.6 mm in length (Figure 7). "Chile, Peru." There are no subsequent records of *Cyclinella* from Chile; its occurrence there in the Recent fauna is unlikely, although the genus is known as a Pliocene or Pleistocene fossil at Mejillones, Antofagasta Province, Chile (23.1°S) (see below). The type locality is here clarified as being Paita, Piura Province, Peru (5.1°S), from where the species is known (CAS 117661).

A. macilenta—Lost. The original figure measures 20 mm in length (Figure 8). (Isla) Salango, Manabí Province, Ecuador (1.6°S); Hugh Cuming, collector.



Figures 4, 5. *Cyclinella producta* (Carpenter, 1856). Figure 4. Holotype of *Cyclina producta*; length = 40.4 mm. Figure 5. Lectotype of *Cyclinella singleyi* Dall, 1902; length = 39.9 mm.



Figures 6–8. *Cyclinella subquadrata* (Hanley, 1844). Figure 6. Lectotype of *Artemis subquadrata*; length, 35.1 mm. Figure 7. Figures of *Venus (Artemis) kroeyeri* Philippi, 1848, from Philippi (1848); length = 27.6 mm. Figure 8. Original figure of *Artemis macilenta* Reeve, 1850; length = 20 mm.

A. saccata—MCZ 169358, holotype, pair; length, 39.8 mm; height, 36.6 mm; width, approximately 20.6 mm (Figure 9). The right valve is intact but cracked; the left valve is now missing its umbones and hinge. Mazatlán, Sinaloa, Mexico (23.2°N); Thomas P. Green, collector.

C. galera—ANSP 13698, holotype, left valve; length, 54.2 mm; height, 52.9 mm; width, approximately 12.5 mm (Figure 10). Puerto Jama (as “Jame”), Manabi Province, Ecuador (0.2°S); Jama Formation; Pliocene.

C. kroeyeri ulloana—CASGTC 06559, holotype, left valve; length, 77.5 mm; height, 73.9 mm; width, approximately 19.3 mm (Figure 11). CASGTC 065560, paratype, left valve; length, 65.4 mm. CASGTC 065561, paratypes; left valve, length, 29.7 mm; right valve, 22.9 mm. Bahía Santa Inéz, Baja California Sur, Mexico (26.9°N), 46 m, sand; Templeton Crocker Expedition station 143-D-4, April 13, 1936.

Description: Shell variable in shape, ovate to subquadrate, length equal to or slightly greater than height ($l/h = 1.0-1.1$; $n = 10$); anterior end evenly to sharply rounded; posterior end rounded to subtruncate; posterior slope set off from central slope by a slightly raised ridge in some specimens; moderately inflated ($l/w = 1.9-2.3$; mean, 2.0; $n = 10$); beaks only moderately inflated. Exterior surface with a thin, tan periostracum. Interior white. Anterior end of pallial line continuous, with a series of smaller scars above it; pallial sinus directed between anterior adductor muscle scar and hinge. Posterior adductor scar positioned well below hinge plate (Figure 18). Posterior cardinals often curved ventrally (straight in some specimens). Length to 81.3 mm (LACM 152576; Cerro Azul, Lima Province, Peru; Figure 16).

Distribution: From the east side of Isla Cedros, Baja California (28.1°N) (LACM 71–92), into and throughout the Gulf of California, to its head at Golfo de Santa Clara, Sonora (31.7°N) (Skoglund Collection), Mexico, south to Cerro Azul, Lima Province, Peru (13.1°S) (LACM 152576; Figure 16). Aside from beach drift, this species has been recorded from the intertidal zone to 75 m (mean 29.2 m; $n = 95$). This is the most common species in collections; I have seen 169 lots, including the types.

This species has been recorded from the late Pleistocene terraces at Newport Bay, Orange County, California (LACM 66-2; Kanakoff & Emerson, 1959:22); on a Pleistocene terrace at Mancora, Tumbes Province, Peru (Bosworth, 1922:177); from the Pliocene or Pleistocene at Mejillones, Antofagasta Province, Chile (D. Frassinetti, e-mail, 24 August 1999); and from the Pliocene at Puerto Jama, Manabí Province, Ecuador (type locality of *C. galera*). The record of “*Cyclina* near *C. subquadrata*” from the Pleistocene of Barbados by Trechmann (1933:36, pl. 4, fig. 4) is more likely to have been based on *C. tenuis* (Récluz, 1852).

Discussion: After considerable sorting and resorting of

the available material, I have come to the conclusion that there is but a single taxon represented by the species names *subquadrata*, *kroeyeri*, *macilenta*, *saccata*, *galera*, and *ulloana*. Indeed, the original figures and the extant type material of these nominal taxa do not represent the extremes of the variability of this species. The types of *A. subquadrata* from Ecuador are small, typical specimens. The original figures of *V. kroeyeri*, presumably from Peru, are very similar. The original figure of *A. macilenta*, also from Ecuador, depicts a specimen that is somewhat narrower anteriorly and expanded posterodorsally, a morphology matched by available specimens. The type specimen of *A. saccata*, from Mexico, is a close match to the type material of *A. subquadrata*, and the type material of *C. ulloana* is simply a large specimen from the Gulf of California. The type specimen of the Ecuadorian Pliocene *C. galera* is thick, with a short anterior end and an expanded posterodorsal margin, and is matched by a Recent specimen from Ecuador (Figure 14).

Four additional specimens of this species are figured here to show the variability in shape exhibited by this species (Figures 12–15). Figure 12 is a typical specimen from the head of the Gulf of California, such as the type material of *A. saccata* and *C. ulloana*. Figure 13 is a large, oval specimen from Panama Bay among the material identified by Olsson (1961) as *C. saccata*. Figure 14 is an Ecuadorian Recent specimen similar in shape to the Pliocene holotype of *C. galera*. Figure 15 is the southern record and size record of the species, a specimen with a subquadrate outline.

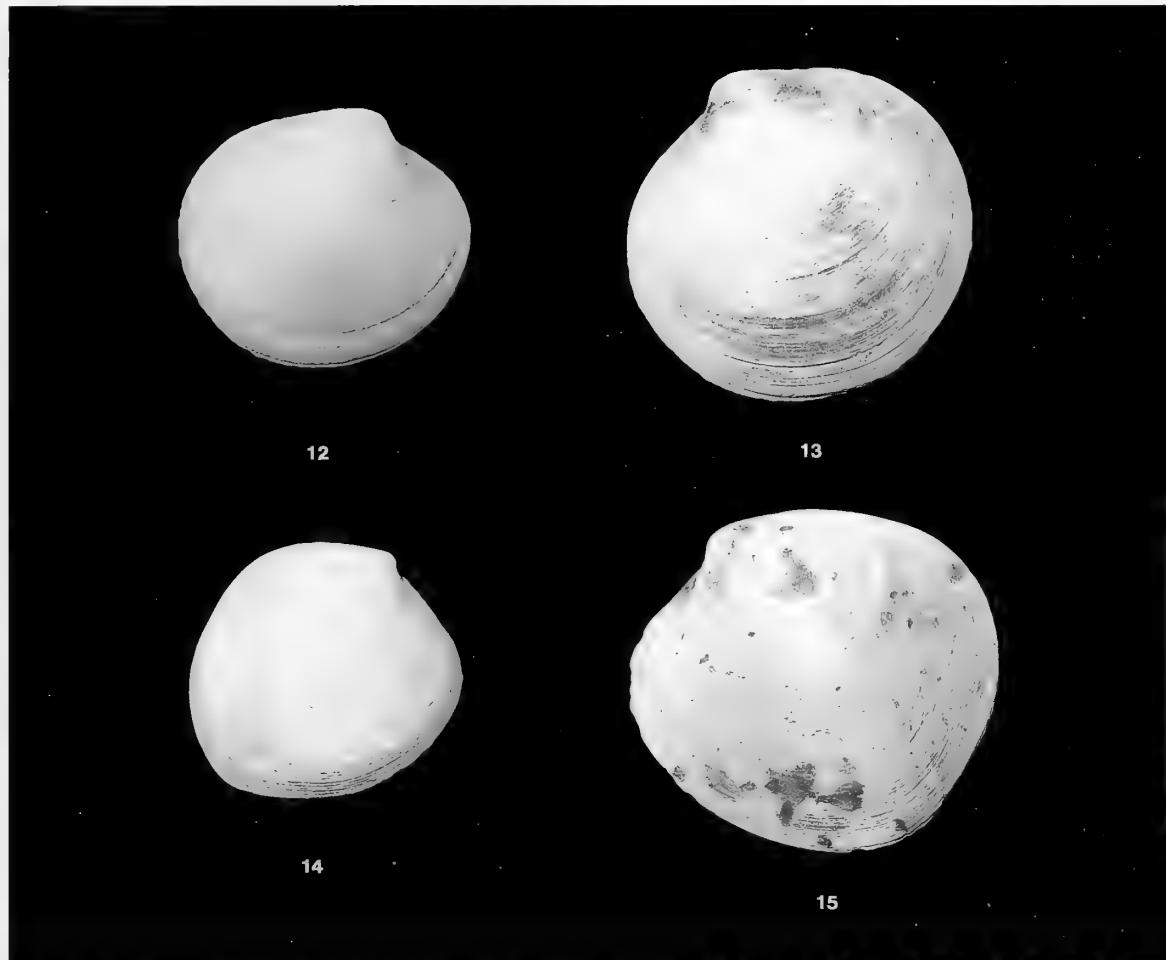
The later-named western Atlantic *Cyclinella tenuis* (Récluz, 1852) is virtually identical to *C. subquadrata* and shows the same pattern of variation in outline. None of the characters that differentiate the three eastern Pacific taxa serves to differentiate them, and I have been unable to find other distinguishing characters. However, the western Atlantic form does not attain as large a size (largest specimen seen: CAS 117674; 41.5 mm; Ponta de Praia, Santos, São Paulo Province, Brazil). This relationship merits additional investigation.

REJECTED RECORDS AND RELATED SPECIES

Artemis turgida Reeve, 1850 (pl. 9, fig. 53), was described from an unknown locality. A slip was later added to the holotype, BMNH 1998194, with a locality of “La Union or Conchagua, Central America, A. Sallé.” Based on a photograph supplied by the BMNH, this species was placed in *Cyclinella* by Fischer-Piette & Vukadinovic (1972:149–151, figs. 13–17). However, examination of the holotype, a pair (length, 28.8 mm; height, 26.7 mm; width, 14.9 mm), shows it to be a *Dosinia*, with an anterior lateral tooth in the left valve, a defined escutcheon, strong commarginal sculpture, and a large, deep pallial sinus. It is more likely that this specimen came from the Indo-Pacific province, because there is no similar eastern Pacific species of *Dosinia*. For example, based on the illustration, it seems very



Figures 9–11. *Cyclinella subquadrata* (Hanley, 1844). Figure 9. Holotype of *Arthemis saccata* Gould, 1851; length = 39.8 mm. Figure 10. Holotype of *Cyclinella galera* Pilsbry & Olsson, 1941; length = 54.2 mm. Figure 11. Holotype of *Cyclinella kroeyeri ulloana* Hertlein & Strong, 1948; length = 77.5 mm.



Figures 12–15. *Cyclinella subquadrata* (Hanley, 1844). Figure 12. SBMNH 345458; Golfo de Santa Clara, Sonora, Mexico; ex Skoglund Coll.; intertidal mud; length = 49.8 mm. Figure 13. UMML 28-2260; Panama Bay at 8.4°N, 79.7°W, in 11–15 m, Panama; length = 71.2 mm. Figure 14. SBMNH 345459; Playas, Guayas Province, Ecuador; trawled; ex Skoglund Coll.; 71.2 mm. Figure 15. LACM 152576; Cerro Azul, Lima Province, Peru; length = 81.3 mm.

similar to *Dosinia (Dosinella) malzini* Fischer-Piette & Vukadinovic, 1972 (pp. 78, 79, pl. 14, figs. 9–13), described from New Caledonia.

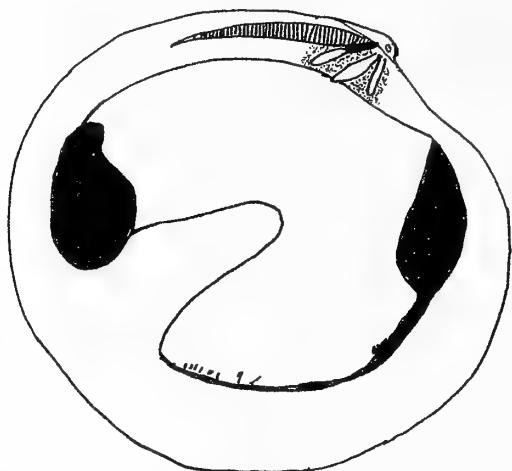
Artemis inflata Sowerby, 1852 (pp. 661, pl. 141, fig. 25), described from an unknown locality and figured only in external view. No type material has been located in the BMNH collection (J. D. Taylor, in Fischer-Piette & Vukadinovic, 1972:148), and it must be regarded as a *nomen dubium* because no diagnostic characters are available.

Artemis tenuis Sowerby, 1852 (p. 661, pl. 141, fig. 22), was described from an unknown locality and figured only in external view. In his original description, Sowerby cited Reeve's figure of *Artemis turgida* (see above). Type material has not been located in the BMNH collection. Two specimens in a lot labeled as possibly being type specimens (BMNH 19990484) are both larger than Sowerby's 16.5-mm-long figure, and neither match it in shape. The larger (length, 22.2 mm) is a small individual of the eastern Pacific *Cyclinella producta* (Carpenter, 1856), and the smaller (length, 20.7 mm) is a spec-

imen of the European *Mysia undata* (Pennant, 1777). Under these circumstances, *Artemis tenuis* Sowerby must either be regarded as a synonym of *Dosinia turgida* (Reeve, 1850) or as a *nomen dubium*. [Because Sowerby's monograph has not been precisely dated, it must be considered to have been issued on 31 December; thus, even if *A. tenuis* Sowerby were considered to be a *Cyclinella*, it would not preoccupy *C. tenuis* (Récluz, 1852), which dates from 1 September.]

Cyclina fragilis Römer, 1860 (pp. 160, 161), has been regarded as a synonym of *Cyclinella tenuis* (Dall, 1902b: 373; Fischer-Piette & Vukadinovic, 1972:139). The distribution of *C. tenuis* was discussed by Boss & Wass (1970); it occurs from Virginia to Brazil. Wright & Moore (1970) studied aspects of its ecology and reproduction. This species is also discussed by Palmer (1927: 408, 409, pl. 24, figs. 3, 5, 18).

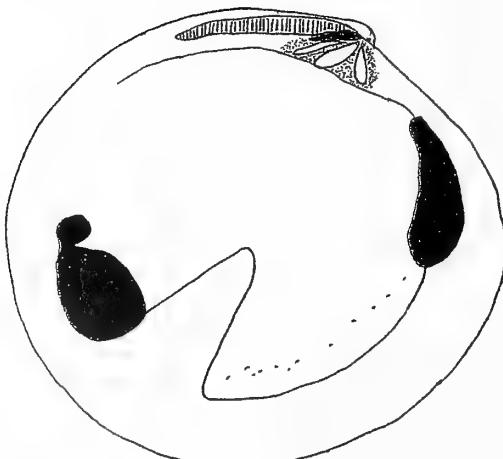
Dosinia (Artemis) tenuis Récluz, 1852 (pp. 250–252, pl. 10, fig. 1, 1'), is the western Atlantic type species of *Cyclinella*. The type specimen of this species is not present in the Muséum d'Histoire Naturelle in Paris (P. Bouchet,



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e-mail, 7 May 1999). The Muséum d'Histoire Naturelle in Geneva holds a specimen that could possibly be the type, although it is slightly larger (length, 38.5 mm) than the originally stated dimensions (length, 35 mm), and it is not accompanied by any convincing documentation (Y. Finet, e-mail, 10 & 12 May 1999).

Fischer-Piette & Vukadinovic (1972:148–149) speculated that *Dosinia minor* Deshayes, 1863 (p. 12, pl. 2, figs. 1–3), described from l'île de La Réunion in the Indian Ocean, might be a *Cyclinella*. It is more likely that it was correctly placed in *Dosinia* in the first place, particularly given its broad, elongate anterior hinge plate. Fischer-Piette & Vukadinovic (1972:149) allocated *Lucina elegans* H. Adams, 1871 (p. 791), to *Cyclinella*. This species, described from the Red Sea, has proven instead to be a synonym of *Wallucina erythraea* (Issell, 1869: 84–85, pl. 1, fig. 9, as *Lucina*) (Oliver, 1992:98, pl. 20, fig. 3a, b). *Lucina elegans* was allocated to *Cyclina* and reported from southeast Asia by Lyngé (1909:251–252, pl. 5, figs. 14, 15). Lyngé's record may be based on some other lucinid, his illustration shows an orbicular shell with fine radial sculpture.

FOSSIL TAXA OF CYCLINELLA

There are several names for fossil *Cyclinella*, particularly from Miocene strata. Given the variability in shape of the Recent *C. tenuis* and *C. subquadrata*, it seems likely that there remain more names than species, even with the synonymies that have thus far been suggested.

Cyclinella cyclia (Guppy, 1866:582, 590, pl. 26, fig. 15a, b; as *Dosinia*) is widely reported in the Miocene of the Caribbean. *Cyclinella gatunensis* Dall, 1903:1285, pl. 52, fig. 18; *C. cyclia domingensis* Pilsbry & Johnson, 1917:200 (see also Pilsbry, 1922:424, 435, pl. 47, fig. 8); and *C. venezuelana* H. K. Hodson, in F. Hodson et al., 1927:59, pl. 34, figs. 3, 4, have been regarded as synonyms (Maury, 1925:151–153, pl. 26, fig. 4; Woodring, 1982:696–697, pl. 120, figs. 18, 19; pl. 123, figs. 3, 4) (see also Palmer, 1927:405–407; 1929:pl. 24, figs. 2, 7, 12, pl. 25, figs. 6, 7, 15, 16).

Cyclinella falconensis H. K. Hodson, in F. Hodson et al., 1927:59, 148, pl. 34, fig. 2, was described from the Oligocene and Miocene of Venezuela.

Cyclinella plasiatenus Woodring, 1925:158–159, 219, pl. 21, figs. 10, 11, was described from the Bowden Miocene of Jamaica (see also Palmer, 1927:408; 1929:pl. 24, figs. 1, 4).

Cyclinella subquadrata guitana Olsson, 1922:243, 287, pl. 31, fig. 8, was described from the Gatun Miocene of Costa Rica (see also Palmer, 1927:408; 1929:pl. 25, fig. 3).

Cyclinella beteyensis Olsson, 1922:242–243, 287, pl. 31, fig. 2, was described from the Gatun Miocene of Costa

Rica, and subsequently recorded from Panama (Olsson, 1964:59, 213, pl. 6, fig. 9) (see also Palmer, 1927:407; 1929:pl. 25, fig. 8).

Cyclinella harrisi Palmer, 1927:407–408; 1929:pl. 45, figs. 6, 7, was described from the Springvale Miocene of Trinidad.

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Anatomy and Histology of a New Species of *Enotepteron* (Cephalaspidea: Gastropteridae) from Tropical Northeastern Australia

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Abstract. The anatomy and histology of a new species of gastropterid cephalaspidean, *Enotepteron heikeae*, sp. nov., from tropical Australia is described. *Enotepteron* is the least documented of the gastropterid genera with only two previously recorded species, from the Yellow Sea (North Pacific) and the Seychelles (Indian Ocean). The unique features of *E. heikeae*, within the genus, are the long thin tail (posterior end of the foot), cuticular penial armature, and a bilobed prostate. The investigation also reveals the presence of a very large anal gland. This gland maybe a useful taxonomic and phylogenetic character not previously recognized. This is the first record of *Enotepteron* from the South Pacific region, and its discovery considerably broadens the previously known geographical occurrence of the genus. Documentation and investigation of this species improves our knowledge of the morphological variation across the genus, and allows reassessment of the generic features to show that the presence of spheres to the posterior edge of the parapodia may be the only unifying character.

INTRODUCTION

The cephalaspidean family Gastropteridae Swainson, 1840, consists of four genera—*Gastropteron* Meckel in Kosse, 1813, *Sagaminopteron* Tokioka & Baba, 1964, *Enotepteron* Minichev, 1967, *Siphopteron* Gosliner 1989—which are distinguished by differences in siphonal and visceral hump formation, the gill, radular teeth, and the male genital complex (Gosliner, 1989; Burn & Thompson, 1998).

The genus *Enotepteron* was established by Minichev (1967) to accommodate a species from the Yellow Sea that was distinct from other described gastropterids. At that time, the generic features were a pair of stalked spheres on the posterior end of the parapodia, inner lateral teeth with a few large denticles, and a lack of penial papilla (Gosliner, 1989). With the addition of a second species to the genus, Gosliner (1988) modified the generic characters to the presence of spheres on the parapodia and the presence of large denticles on the inner lateral teeth. A phylogenetic review of the Gastropteridae (Gosliner, 1989) supported recognition that *Enotepteron* is a valid genus and that further generic apomorphies include the absence of a shell and an appressed cerebral ganglion.

Therefore only two species of *Enotepteron* have previously been described, *E. flavum* Minichev, 1967, from

the Yellow Sea, and *E. rosewateri* Gosliner, 1988, from Aldabra Atoll in the Seychelles. This present paper describes a new species of *Enotepteron* from tropical Australia. This is the first record of a member of this genus from the South Pacific region. Organ systems of this species are examined by macroscopic dissection as well as detailed histological investigation.

MATERIALS AND METHODS

Specimens of *Enotepteron heikeae* were collected by plankton tow in Cleveland Bay, a shallow, sheltered coastal bay along the northeastern coast of Queensland, Australia. Animals may have been swimming in the lower water column after being disturbed, or accidentally scraped from the muddy benthos. Five specimens in total from Cleveland Bay were examined. Live animals were videotaped before two specimens were preserved in 8% formalin in seawater, and three specimens in 70% alcohol. One alcohol-preserved specimen was dissected; one formalin-preserved specimen was sectioned (2.5 µm) using Kulzer methyl-methacrylate resin and toluidine blue stain. The radula was scanned using a Hitachi Scanning Electron Microscope. Terminology used in anatomical descriptions follows Wägele & Willan (2000).

RESULTS

Enotepterion heikeae

Brodie, Klussmann-Kolb & Gosliner, sp. nov.
(Figures 1–3)

Type material: Total of five specimens, all 5 mm preserved length, Cleveland Bay, Queensland, Australia ($19^{\circ}18'S$, $146^{\circ}58'E$) 3 August 1994 (1) Holotype: 1 specimen (Queensland Museum Townsville [QMT], Australia Reg. No. MO40196), (2) Paratypes: 1 specimen (Queensland Museum Townsville, Australia Reg. No. MO40197); 1 specimen, histological sections (methacrylate resin) (Queensland Museum Townsville, Australia Reg. No. MO40198); 2 specimens, 1 dissected (California Academy of Sciences, San Francisco, USA Reg. No. CASIZ 121556); 1 specimen, intact (California Academy of Sciences, San Francisco, USA Reg. No. CASIZ 121557).

Etymology: This species is named in honor of PD Dr. Heike Wägele of the Ruhr-Universität Bochum (previously of the University of Bielefeld) for her contributions to opisthobranch systematics and phylogeny, particularly with respect to encouragement and support to graduate students.

Distribution: To date, this species is only known from Cleveland Bay, Townsville, Australia.

External morphology: The living animals at rest (Figure 1A) are 3–6 mm in length, and 6–7 mm in diameter when their parapodia are spread. The body color is translucent off-white with small brownish orange, and larger black, irregular markings. Anteriorly the cephalic shield is broad. When raised, the posterior of this shield produces a “siphon,” the edges of which form an open groove. This “siphon” is often held upright when the animal is crawling but held forward and flattened when the animal is swimming. A siphonal crest or papillae is absent. No flagella are present on the body, but a pair of flexible stalked spheres, with variable patches of black pigment on the rounded apex, is present on the inside posterior of the parapodia. These spheres are folded in beneath the parapodia when the animal is at rest. A long, very thin “sting-ray-like” tail is also present as a posterior extension of the foot. The gill of the dissected specimen consists of nine simple plicae. No shell was found in any of the specimens examined.

Internal morphology:

Digestive system. A schematic diagram of the relatively simple digestive system is shown in Figure 1B. The small rounded mouth opens into the short oral tube. The epidermal tissue of the mouth opening is folded and heavily ciliated. Numerous pear-shaped subepidermal glandular cells are present with small dark-blue-staining nuclei. The content of these cells is probably mucus. Dark-blue-stain-

ing glandular cells containing small granules are also visible subepidermally.

The oral tube expands into a relatively large pear-shaped muscular pharynx. The epithelium of the oral tube is folded, surrounded by muscle, and composed of barely discernible cuboidal cells. A few subepidermal glandular cells are visible. These cells contain light-red-staining mucus secretions.

The pharynx (as defined by Wägele & Willan, 2000) is elongate anteriorly, but becomes wider toward its posterior end. At the transition between the oral tube and the pharynx the epithelium is covered by a very thin cuticle, which is barely visible in some parts (Figure 2A).

Two small jaw plates, bearing numerous irregular rodlets (Figure 3A) are located at the anterior end of the pharynx. The radular formula of the dissected specimen is $18 \times 4.1.0.1.4$. The inner lateral teeth are broad with seven to nine irregular denticles (maximum height $6\ \mu\text{m}$) on the inside of the large cusp (Figures 3B,C). The outer laterals have a prominent cusp but lack denticles along the masticatory margin (Figure 3D).

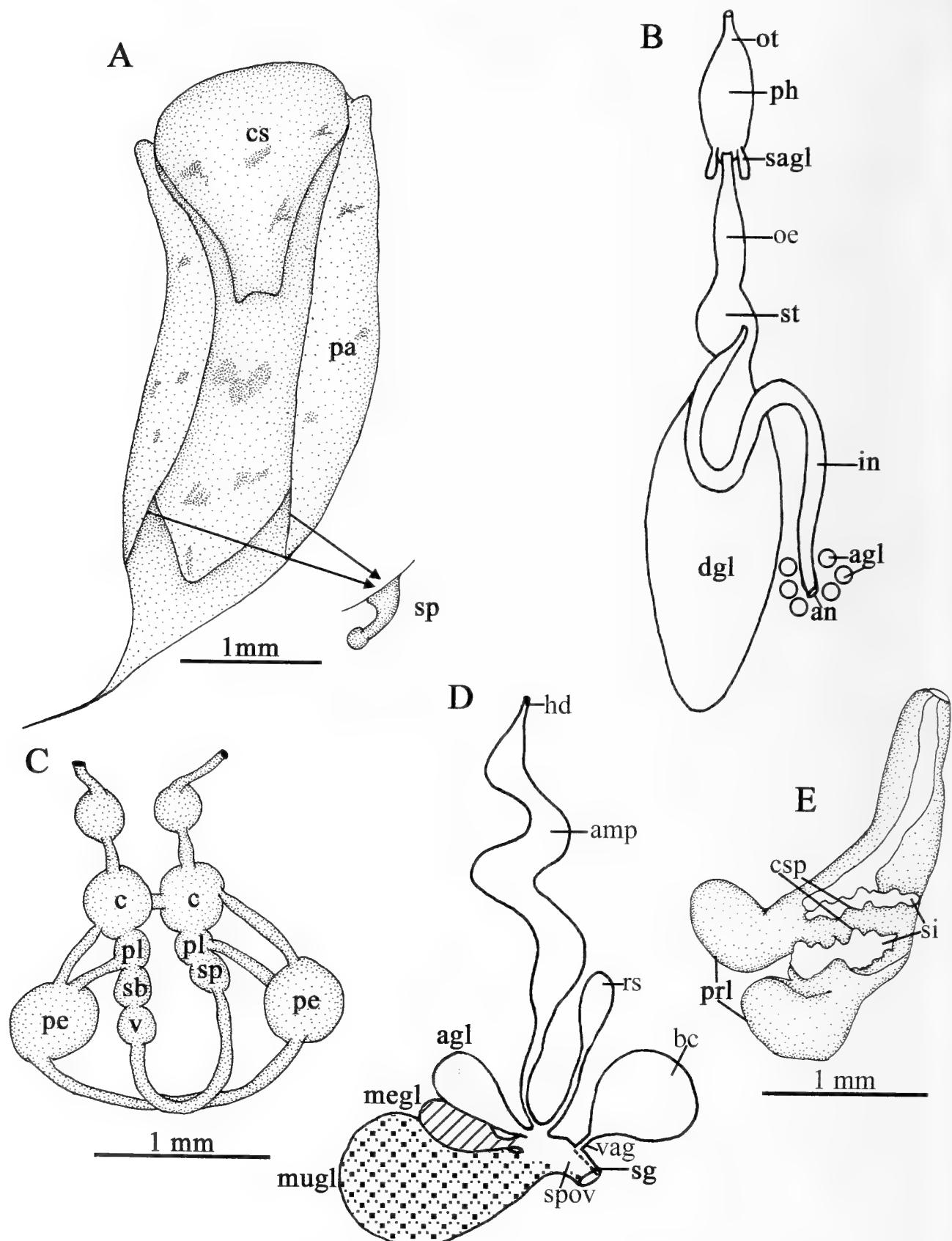
A pair of salivary glands emerges, one on each side of the posterior pharynx, at the transition of the pharynx into the esophagus, and runs posteriorly along the anterior portion of the esophagus (Figure 1B). Salivary gland cells are ciliated, with light staining granules and a large nucleus. A nucleolus is sometimes also visible. A few columnar cells surround a common central duct (Figure 2B).

The tubular esophagus is narrower than the pharynx (Figure 1B) but has a relatively large lumen. The epithelium is composed of columnar glandular cells with elongate apices. These cells contain large nuclei, and in some cells mucus secretions are visible. The epithelium is surrounded by a muscle layer. The rounded stomach is differentiated from the esophagus by possession of a thin epithelium without glandular cells.

The long uniform intestine leaves the stomach at the latter's junction to the digestive gland and emerges on the right side. The folded intestinal epithelium is composed of cuboidal cells with centrally lying nuclei. These cells bear long cilia.

The anal opening is on the right-hand dorsal side just behind the gill. The epithelium of this opening is folded with long cilia. Within the connective tissue the anal opening is surrounded by a relatively large number of irregularly shaped glandular cells that contain numerous heterogeneous secretions and dark-blue-staining nuclei. A histological section of this large distinct anal gland is shown in Figure 2C. The presence of glandular secretions within the anal opening suggests that these glandular cells are discharging inside the anal opening.

The long unilobed digestive gland is composed of one main central canal, which is lined by glandular epithelium consisting of several cell types that are difficult to distinguish. Some cells are elongate and have a club-shaped apical tip, whereas others are columnar. Some cells con-



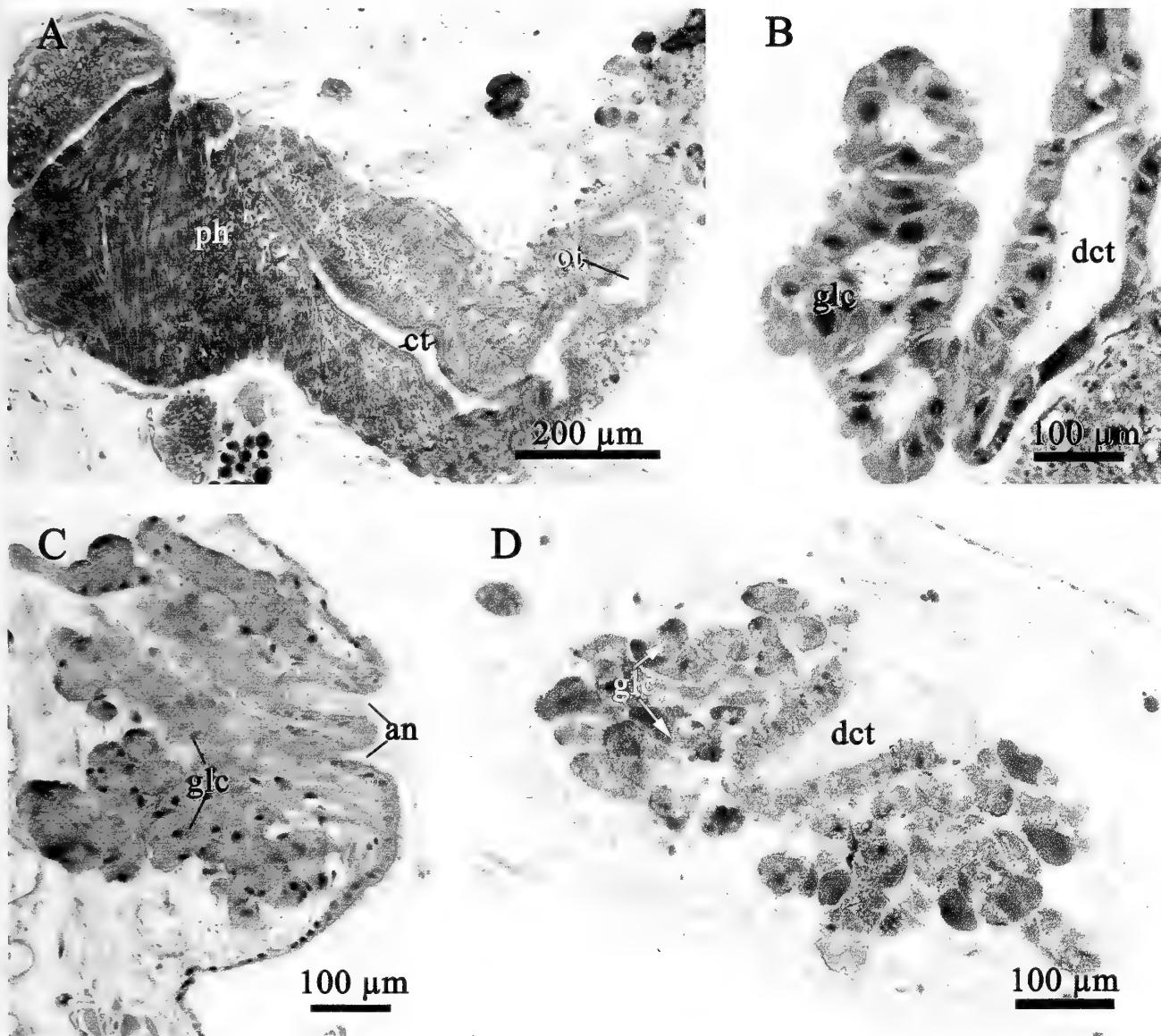


Figure 2. *Enotepteron heikeae* Brodie, Klussmann-Kolb & Gosliner, sp. nov. Histological sections of specimen QMT M040198. A. Transition between the oral tube and the pharynx showing a very thin cuticle covering the epithelium. B. Salivary gland showing central common duct and glandular cells. C. Anal gland and anus showing long cilia around the anal opening. D. Foot (pedal) gland showing pear-shaped glandular cells arranged around a large ciliated duct. an = anus, ct = cuticle, dct = duct, glc = glandular cell, ot = oral tube, ph = pharynx.

←

Figure 1. *Enotepteron heikeae* Brodie, Klussmann-Kolb & Gosliner, sp. nov. A. Composite drawing of live individual. cs = cephalic shield, pa = parapodia, sp = spheres. B. Schematic outline of the digestive system (QMT M040198). agl = anal gland, an = anus, dgl = digestive gland, in = intestine, oe = esophagus, ot = oral tube, ph = pharynx, sagl = salivary gland, st = stomach. C. Drawing of the central nervous system (CASIZ 121556). c = cerebral ganglion; pe = pedal ganglion; pl = pleural ganglion; sb = subintestinal ganglion; sp = supraintestinal ganglion; v = visceral ganglion. D. Schematic outline of the anterior reproductive system (QMT M040198). agl = albumen gland, amp = ampulla, bc = bursa copulatrix, hd = hermaphroditic duct, megl = membrane gland, mugl = mucus gland, rs = receptaculum seminis, sg = sperm-groove, spov = spermiduct, vag = vagina. E. Drawing of the copulatory organ (penis) (CASIZ 121556). csp = cuticular spines, prl = prostatic lobes, si = sinuses.

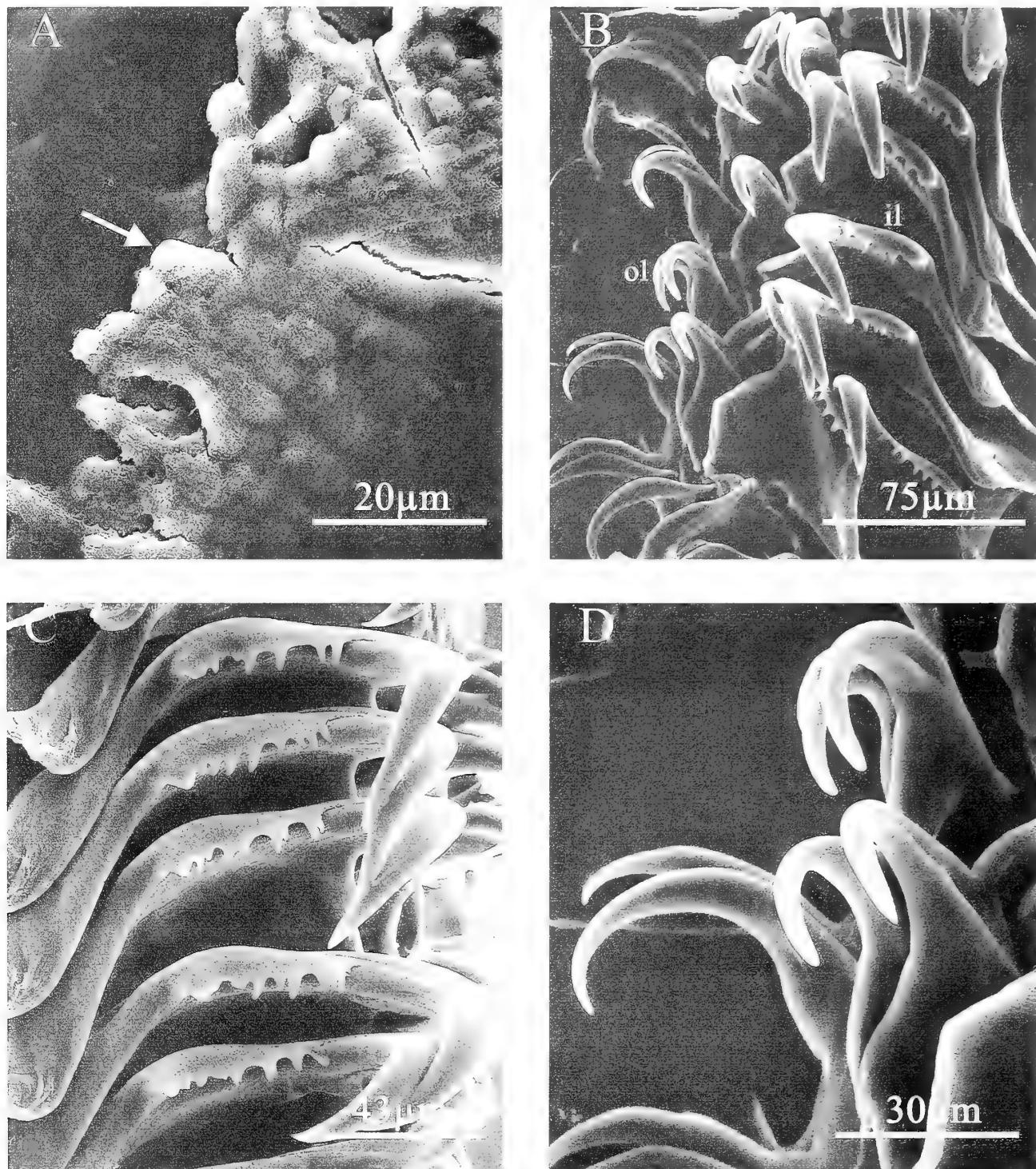


Figure 3. *Enotepteron heikeae* Brodie, Klussmann-Kob & Gosliner, sp. nov. Scanning electron micrographs of jaws and radula teeth (CASIZ 121556). A. Jaw plate showing irregular rodlets (see arrow). B. Several rows of radular teeth showing the difference between the inner and outer lateral teeth across a row. ol = outer lateral, il = inner lateral. C. A close-up of the inner lateral teeth showing seven to nine irregular denticles on the inner border. D. Close-up of the outer lateral teeth showing absence of denticles on the smoothly curved cusp.

Table 1

Features of *Enotepteron heikae* in comparison with all other known members of the genus
Enotepteron and *Gastropteron bicornutum* which displays similar coloration.

Species	Distribution	Depth found	Body color	Shell	Flagellum	Gill plicae	Spheres	Tail	Jaws
<i>Enotepteron heikae</i>	northern Australia	<4 m	Translucent off-white, with small brownish orange and larger black irregular markings	absent	absent	9 simple	stalked	long, very thin, tapering	well developed
<i>Enotepteron flavum</i>	Yellow Sea	28 m	Uniform yellow (preserved material only)	absent	present	8–10 simple	stalked	short pointed	well developed
<i>Enotepteron rosewateri</i>	Seychelles	intertidal	Translucent white, with orange and brown markings	absent	variable, short or absent	3–4 simple	sessile	short rounded	poorly developed
<i>Gastropteron bicornutum</i>	Japan & Papua New Guinea	6.8 m	Translucent white with black, opaque white, and yellow pigment	present	2 present	12–18 bipinnate	absent	long, thin, elongate	well developed

Species	Radula formula	Inner lateral teeth	Anal gland	Cerebral commissure	Visceral ganglion	Penial papillae	Prostate	Reference
<i>Enotepteron heikae</i>	4.1.0.1.4	7–9 irregular denticles	present large	short	distinct	not distinct, cuticular armature	two separate glandular lobes	This study
<i>Enotepteron flavum</i>	3.1.0.1.3	regular denticles	absent	short	fused	absent	simple	Minichev 1967; Carlson & Hoff 1974; Gosliner 1988, 1989
<i>Enotepteron rosewateri</i>	3.1.0.1.3	3–6 irregular denticles	?	short	distinct	simple, unarmed	thick, simple, curved, glandular	Gosliner 1988
<i>Gastropteron bicornutum</i>	4.1.0.1.4	5–11 regular elongate denticles	?	short*	distinct	simple, short, unarmed	simple, curved	Baba & Tokioka 1965; Gosliner 1989

* incorrectly scored "long" in Gosliner (1989) Table 2

tain non-staining vacuoles, while others contain blue-green or dark-blue-staining granules. In some cells, mucus droplets are visible. The epithelial lining of the central digestive canal is not glandular throughout. Some areas, mainly the ventral anterior portion, are composed of cuboidal cells.

Gill. The simple gill plicae have a very thin epithelium of cuboidal cells with central nuclei; the epithelium is ciliated and encloses large cavities, which appear to be empty.

Foot (Pedal) Gland. A gland is present at the posterior of the foot below the base of the tail. The pear-shaped glandular cells, with pink staining contents, are arranged around a ciliated duct (Figure 2D), which opens to the outside of the foot.

Nervous System. All the ganglia are contained within a circum-esophageal nerve ring (Figure 1C). The cerebral ganglia are appressed with a very short commissure. The visceral ganglion is distinct.

Reproductive System. The anterior part of the gonad lies on top of the digestive system and extends to the far end of the body cavity. The gonad, which is surrounded by connective tissue, is composed of follicles with sperm acini separated from smaller oocyte follicles. Sperm acini are located centrally, surrounded by oocyte follicles. Oocyte follicles are subdivided into cells containing nucleus, yolk granules, and non-staining vacuoles. Sperm acini contain both immature spermatogonia and mature sperm. The heads of the mature sperm face the epithelial lining, and some nursing cells are present.

A schematic diagram of the monaulic reproductive system is shown in Figure 1D. The hermaphroditic duct is short and hardly differentiated from the ampulla. *In situ*, the tubelike ampulla is coiled and runs from the ventral part of the gonad on the right side of the digestive gland toward the anterior reproductive system. The ampulla itself is lined by an epithelium composed of cuboidal cells with central nuclei of elliptical shape. This epithelium is heavily ciliated in certain areas. Within the ampulla, sperm are arranged irregularly, i.e., not aligned, with heads facing the epithelium.

The seminal receptacle has an elongate club shape. The thin duct leading to it is relatively long. The epithelium of the receptacle is weakly folded and surrounded by a layer of muscle. The epithelium consists of ciliated cuboidal cells with small hardly visible nuclei. Sperm are present in the seminal receptacle of the specimen sectioned, and these are arranged in the usual way with heads facing the epithelium. The duct leaving the receptacle is also lined by a ciliated epithelium of small cuboidal cells. The sectioned animal has probably copulated, since sperm is visible in the receptacle.

The bursa copulatrix (= gametolytic gland) is globular and connects to the distal section of the spermiduct, close to the genital opening, via a short thin vagina (allo-sperm receiving duct). The vaginal epithelium consists

of cuboidal cells, with small nuclei, bearing long cilia. Nucleoli are also visible in these cells. The bursa copulatrix is lined by an epithelium of cuboidal cells with basally lying nuclei. This epithelium bears short cilia and contains numerous non-staining vacuoles. The epithelium of the spermiduct consists of cuboidal cells containing small nuclei and long cilia.

The nidamental glandular system is divided into three separate parts (Figure 1D). The small proximally lying albumen gland consists of one lobe. Like the membrane gland and the distally lying mucus gland, the albumen gland joins the spermiduct at its distal end. The albumen gland is composed of high columnar glandular cells (which are smaller than those seen in the mucus gland) containing numerous small dark-blue-staining granules and a basally lying nucleus. Supporting cells are not visible, but cilia are present. Following the albumen gland is a small membrane gland, composed of columnar cells containing heterogeneous mucous fibers, which stain pink. The supporting cells in the membrane gland bear long cilia. The distally lying mucus gland is the largest of the nidamental glands. It is widely folded and consists of highly columnar glandular cells with different mucus contents. The staining properties range from red to violet. The supporting cells in the mucus gland bear short cilia.

A sperm-groove leads from the spermiduct to the prostate and penis. The sperm-groove is a fold in the outer epithelium, which is lined by long cilia. No glands are associated with this groove. The penis opens to the outside at the anterior of the body next to the mouth. There are two separate glandular prostatic lobes (Figure 1E). The penial papilla is not distinct. Some unusual cuticular spines are arranged around two sinuses. These spines are not well developed nor are they arranged in distinct rows.

Excretory System. The kidney is located on top of the digestive gland and anterior portion of the gonad. It is lined by pavement epithelium with basal nuclei and large non-staining vacuoles with unknown contents. The epithelium forms internal folds lining a large lumen. The reno-pericardial duct is small, narrow, and ciliated. It leads to the nephropore, which is located on the right side of the body underneath the very posterior end of the gill.

Circulatory System. The pericard is lined by very thin pavement epithelium. The atrium and ventricle are composed of loose connective tissue, and located left of the kidney on top of the digestive gland.

Behavior: This species is an active swimmer. The swimming action involves rapid beating of the parapodia in a very "batlike" manner. The posterior of the cephalic shield is flattened during this swimming behavior.

DISCUSSION

Within the genus, *Enotepteron heikeae* is unique in having a long, very thin tail, cuticular penial armature, and

a bilobed prostate. Table 1 presents a comparison of *E. heikeae* with other *Enotepteron* species and *Gastropteron bicornutum* Baba & Tokioka, 1965, which it resembles in color.

Enotepteron flavum differs from *E. heikeae* in that it has a short pointed tail, regular denticles on the inner lateral teeth, a fused visceral ganglion, no penial papillae, a simple prostate, and quite possibly no anal gland. *Enotepteron rosewateri* differs from *E. heikeae* in that it has sessile parapodial spheres, a short rounded tail, poorly developed jaws, unarmed penial papillae, and a simple prostate.

Enotepteron heikeae resembles *E. flavum* in that the parapodial spheres are stalked, whereas in *E. rosewateri* they are sessile. Burn (1980) considered that the right-hand sphere probably functions to hold a partner's penial papilla in place during copulation, whereas the left-hand sphere is the result of bilateral symmetry. Gosliner (1989) however, considered this unlikely because *E. flavum* lacks a penial papilla. Such a hypothesis needs to be substantiated by observation of living animals during mating. Our histological investigations reveal no internal structural components that suggest any particular function to these appendages.

In coloration *E. heikeae* closely resembles *Gastropteron bicornutum*. However, unlike *G. bicornutum*, our species has no shell, lacks hornlike protuberances (flagella) on the dorsal hump, has simple rather than bipinnate gill plicae, carries spheres on the inner posterior of the parapodia, and has a tapering tail and irregular denticles on the inner lateral teeth. Also, *G. bicornutum* has a simple short, unarmed penial papilla and a simple curved prostate, whereas *E. heikeae* has an indistinct penial papilla, unusual cuticular spines around two sinuses, and two separate prostatic lobes.

Minichev (1967) conducted a histological study of *Enotepteron flavum*. He found that *E. flavum* has subepithelial basophilic and acidophilic glands surrounding the oral tube and a stomach not distinctly separated from the esophagus. A foot gland is also present in *E. flavum*. It is notable that Minichev did not report an anal gland. Considering the very conspicuous nature of this gland in *H. heikeae*, its presence may well be an additional unique character of the current species. According to Wägele & Willan (2000), anal glands are not widespread within the Opisthobranchia.

According to Gosliner (1989), the presence of spheres on the parapodia and the presence of large denticles on

the inner lateral teeth characterize *Enotepteron*. Other apomorphies are stated to include an absence of shell and an appressed cerebral ganglion. Our investigations confirm that a characteristic feature of the genus is the spheres on the posterior parapodia but show that the denticles on the inner lateral teeth are not particularly large. In fact the inner lateral denticles of *E. heikeae* (this study Figure 3C) and *E. rosewateri* (see Gosliner, 1988: figure 14A) are smaller than those found in *Gastropteron bicornutum* (see Gosliner, 1989: figure 24). Thus, the only remaining unique generic character for *Enotepteron* appears to be the presence of spheres to the posterior edge of the parapodia.

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Reproductive Cycle of the Clam *Tellina petitiana* d'Orbigny, 1846, in Nuevo Gulf (Argentina)

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Abstract. *Tellina petitiana* inhabits the intertidal and upper subtidal zones of the Atlantic coast of South America, from Rio do Janeiro to northern Patagonia. Its gonads are diffuse and the sex cannot be detected with the naked eye. The application of histological techniques to individuals collected monthly for one year from a locality at the southern limit of the species distribution (Puerto Madryn, 42°46'S, 65°02'W) revealed a sex ratio not significantly different from 1:1 and no record of hermaphroditism. At vitellogenic maturity the oocytes reach a maximum diameter of approximately 70 µm and are surrounded by a dense basophilic substance of fibrous appearance. The spermatozoa, 16 µm in length, show a patchy distribution within the internal space of the alveoli. This species is iteroparous and displays an extended spawning period, from late spring to summer. Most specimens were in regression throughout fall, in multiplication from late fall to winter, and in maturation during spring. The development of the gonadal tissue was maximal in December and minimal in April. The yolk accumulation started in September. The vitellogenic oocytes reached their maximal estimated mean diameter in January and were present in few animals in March.

INTRODUCTION

Tellina petitiana d'Orbigny, 1846, inhabits sandy-muddy bottoms of the intertidal and upper subtidal of the Atlantic coast of South America from 23°S to 43°S, and is common in the gulfs of northern Patagonia (Castellanos, 1967; Rios, 1975; Scarabino, 1977; Barón, 1995). In some areas, the species is an important food item of scolopacid birds during inter-hemispherical migration (from February to April; Pagnoni, 1997).

Several descriptions of the reproductive cycle of tellinids from the Northern Hemisphere have been published to date (Lammens, 1967; Rae, 1978; Salzwedell, 1979; Brousseau, 1987; Harvey & Vincent, 1989; Kawai et al., 1993). However, the reproductive cycle has not been studied in tellinids from the southwest Atlantic.

The morphology and anatomy of *T. petitiana* have been reported in detail (Barón & Ciocco, 1997, 1998; Ciocco & Barón, 1998). The species is gonochoric, and its gonads have been characterized as "diffuse," macroscopically evident only at sexual maturity (Barón & Ciocco, 1998). The aim of this paper is to describe the reproductive cycle of the species for the first time.

MATERIALS AND METHODS

Samples of *Tellina petitiana* were randomly collected from the lower intertidal and upper meters of the subtidal

of a fine and medium grain sandy beach with low step (1.21°; Escofet, 1983) and semidiurnal tidal regime (average amplitude: 4.69 m), located at the waterfront of the city of Puerto Madryn (Mimosa Beach; 42°46'S, 65°02'W; Figure 1).

Twenty individuals of intermediate shell lengths were sampled once per month from April 1993 to March 1994. Once extracted from the sediment by digging and sieving, the clams were fixed in 10% formaldehyde in seawater and dehydrated in consecutive baths of 96% ethanol and a 1:1 mixture of 100% ethanol and xylene. Finally, 5 µm thick sections were cut with a microtome and stained with eosin-hematoxylin and Masson's trichromic stains.

Histological observations were made on the gonads. Cells from the germ line were observed under a microscope with a ×100 immersion objective, identified according to their size, shape, and arrangement, and photographed. Sex ratio was estimated from the total sample (n = 240), and a Chi-square test was used to verify differences from a 1:1 proportion. Gametogenesis was described according to the morphology of the cells observed. A scale of gonadal maturity was developed for *T. petitiana*, based on the stages assigned to the tellinids *Macoma balthica* (Linnaeus, 1758) (Lammens, 1967); *Macoma secta* (Conrad, 1837) and *Macoma nasuta* (Conrad, 1837) (Rae, 1978); *Tellina fabula* Gmelin, 1791 (Salzwedell, 1979); and *Tellina nitidula* (Dunker, 1860) (Kawai et al., 1993); and other bivalves, including *Aequipecten tehuelchus* (d'Orbigny, 1846) (Lasta & Calvo, 1978,

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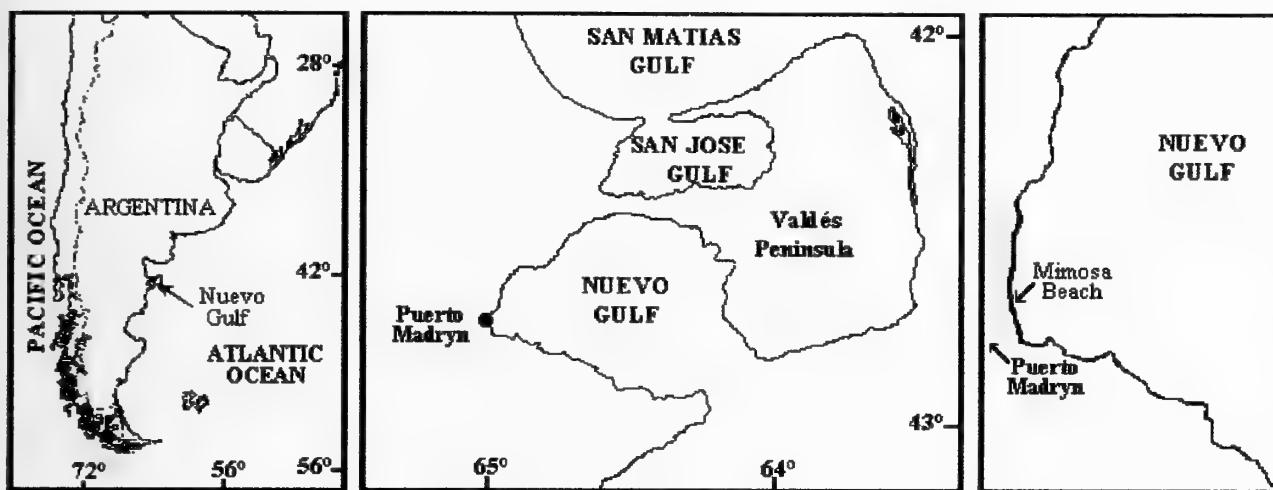


Figure 1. Location of the study area.

as *Chlamys tehuelcha*); *Protothaca asperrima* (Sowerby, 1835) (Palacios et al., 1986); *Spisula solidissima* (Dillwyn, 1817); *Arctica islandica* (Linnaeus, 1767) (Jones, 1981); and *Spisula solidissima similis* (Say, 1822) (Kanti et al., 1993).

The sequence of gonadal stages was analyzed by comparing the percentages of specimens in different stages of maturity in the consecutive monthly samples. This process was compared with the percentage of alveolar area (PAA; Lasta & Calvo, 1978), an index reflecting the area occupied by gonadal alveoli relative to total area among the somatic organs (maximum area available for gonadal development) in histological sections. PAA was estimated for each individual from two microscopic fields under 10 × 10 magnification. A total of 480 fields were drawn on paper with a camera lucida. The outlines obtained were scanned (118 × 118 pixels/cm²) and the inter-alveolar and intra-alveolar areas were calculated by pixel counting (Aldus Photo Styler 2.0). The maturity index was then estimated as PAA = (intra-alveolar area × 100)/total (inter-alveolar + intra-alveolar) area, following Lasta & Calvo (1978).

Additionally, monthly frequency distributions of vitellogenic oocyte diameters were estimated from September to February, the time period in which this cell type was present in the gonads. Due to the diversity of forms adopted by the vitellogenic oocytes during the process of maturation, the diameters were estimated through an adaptation of the technique used by Laruelle et al. (1994). The outlines of approximately 50 vitellogenic oocytes per clam were drawn from the histological sections under 100 × 10 magnification (immersion objective). Based on the assumption that each oocyte has the nucleolus placed in its center (Kennedy & Battle, 1964; Laruelle et al., 1994), only the cell sections showing this structure were selected to estimate oocyte diameters. The area delimited by each

outline was estimated with the technique used to calculate the PAA. Each area was treated as if it were the surface of a section passing through the center of a sphere, and the diameter of each oocyte was then estimated as $d = 2\sqrt{(area/\pi)}$. As a matter of comparison, a correlation analysis was performed between the average oocyte diameter per individual and the square root of the corresponding PAA.

For the sampling period, monthly means of surface water and air temperature recorded on an hourly basis were obtained from the Servicio de Hidrografía Naval de la Armada Argentina (1500 m from the sampling site) and the Servicio de Física Ambiental del Centro Nacional Patagónico, respectively. This information was supplemented with historical temperature registers supplied by the same institutions.

RESULTS

Sex Ratio

From a total of 240 individuals observed, 126 were females and 114 males. In the size range explored (33–40 mm), sex ratio did not significantly differ from 1:1 (Chi square test, $P = 0.44$, df = 1). No hermaphrodites were found.

Gametogenesis Characterization

Oogenic Series. In the females, primary germ cells (g, Figure 2), 10–12 µm in diameter (d), are imbricated in the alveolar walls and have a clear and light eosinophil cytoplasm and rounded nucleus ($d = 5–6 \mu\text{m}$) with the chromatin arranged as dispersed basophilic fragments. Oogonia 1 (o1, Figures 2,3) are adherent to the alveolar walls and have a similar appearance to that of the germlinal cells. The nucleus ($d = 3–4 \mu\text{m}$) is clear and oc-

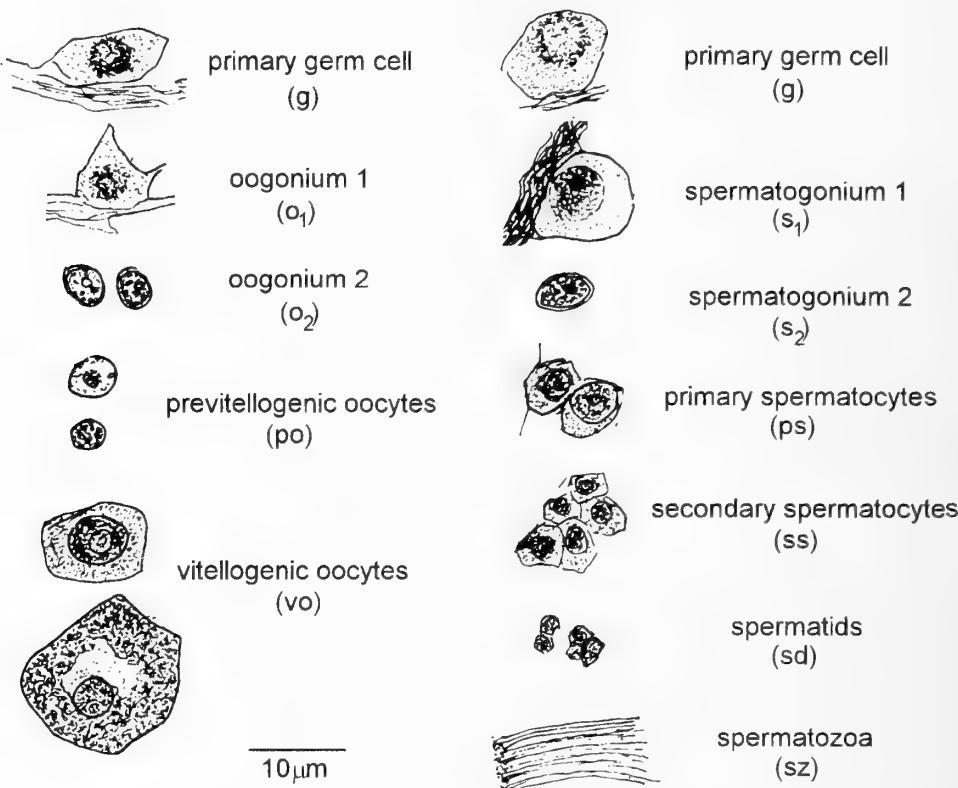
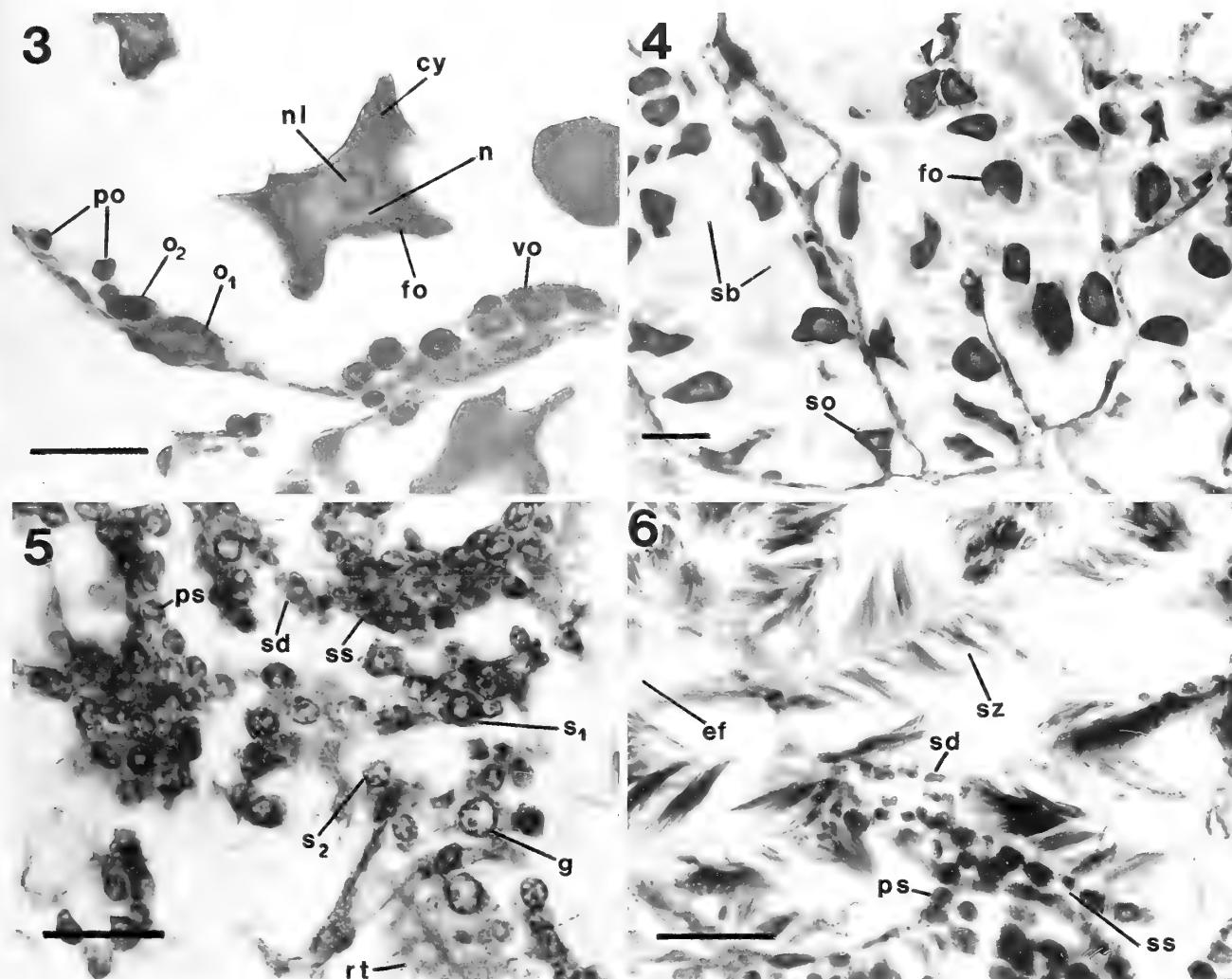


Figure 2. Schematic drawing of the sequence of gametogenic stages of *Tellina petitiana*. Left: oogenesis; right: spermatogenesis.

cuples a substantial part of the cell's section. Oogonia 2 (o_2 , $d = 3 \mu\text{m}$, Figures 2,3) have scarce cytoplasm. Previtellogenic oocytes (po, $d = 6 \mu\text{m}$, Figures 2,3) have basophilic nucleus and cytoplasm and are often tightly clustered, so that the plasmatic membranes take shapes ranging from rounded to polyhedral. Vitellogenic oocytes (vo, Figures 2,3) accumulate reserve substances, significantly increasing their size. These cells remain adherent to the alveolar walls until they reach approximately $20 \mu\text{m}$ in diameter. From this size up, cells start to detach, progressively taking stalked shapes and irregular outlines (so, Figure 4). Vitellogenic oocytes increase their diameter until they reach 40 to $75 \mu\text{m}$; their outlines become rounded, and their stalks become long, slender, and hardly detectable. In section these cells appear free in the alveolar lumen, even when they may still be attached to the alveolar walls by a thin stalk (fo, Figures 3, 4). Vitellogenic oocytes have acidophil cytoplasm (cy, Figure 3), a clear nucleus (n, Figure 3), and a conspicuous nucleolus (nl, Figure 3). Among the stalked (so, Figure 4) and free oocytes (fo, Figure 4) it is possible to observe a basophilic substance of fibrous aspect, occupying most of the intra-alveolar spaces (sb, Figure 4). This substance is dense, indistinguishable with Masson's trichromic staining, and can deform the oocytes when the intra-alveolar space is limited.

Spermatic Series. In males, primary germ cells ($d = 8-9 \mu\text{m}$) lie within the alveolar wall epithelium, and display a clear cytoplasm and a basophilic nucleus (g, Figures 2,5). Spermatogonia 1 (s_1 , $d = 7 \mu\text{m}$, Figures 2,5) remain attached to the alveolar walls and present a clear nucleus, with condensed chromatin of reticular aspect. Spermatogonia 2 (s_2 , Figures 2,5) are similar to spermatogonia 1, but their cytoplasm consists of a thin ring surrounding the nucleus. Primary spermatocytes (ps , $d = 6 \mu\text{m}$, Figures 2,5) have clear and very scarce cytoplasm, and a deeply basophilic nucleus. These cells are always crowded and their walls show hexagonal contours. Secondary spermatocytes (ss, Figures 2,5) show the same characters as primary spermatocytes, but are smaller ($d = 4 \mu\text{m}$). Spermatids (sd, Figures 2,6) are deeply basophilic cells ($d = 2 \mu\text{m}$), with no perceivable cytoplasm. Spermatozoa (sz, Figures 2,6) measure $16 \mu\text{m}$ in length and are heavily basophilic. The reticular tissue (rt, Figure 5), formed by "follicular cells," according to other authors' terminology (Coe, 1943; Lammens, 1967; Rae, 1978; Borzone, 1989), delimits several compartments within the alveoli of *T. petitiana*. In each compartment it is possible to observe the different cellular types of the spermatic series lined up with the spermatozoa placed in the lumen, forming dense cell packs.



Figures 3–6. Appearance of female and male germ lines' cells. Figure 3. Detail of the female series. Figure 4. Alveoli containing mature oocytes. Figure 5. Detail of the first cellular stages of the male series. Figure 6. Detail of the advanced cellular stages of the male series. Key: cy, cytoplasm; ef, eosinophil fibers; fo, free oocyte; g, primary germ cell; n, nucleus; nl, nucleolus; o₁, oogonia 1; o₂, oogonia 2; po, previtellogenic oocyte; ps, primary spermatocyte; rt, reticular tissue; s₁, spermatogonia 1; s₂, spermatogonia 2; sb, basophilic substance; sd, spermatid; so, stalked oocyte; ss, secondary spermatocyte; sz, spermatozoa; vo, vitellogenic oocyte. Figures 3, 5, 6: scale bar = 20 μ m; Figure 4: scale bar = 50 μ m.

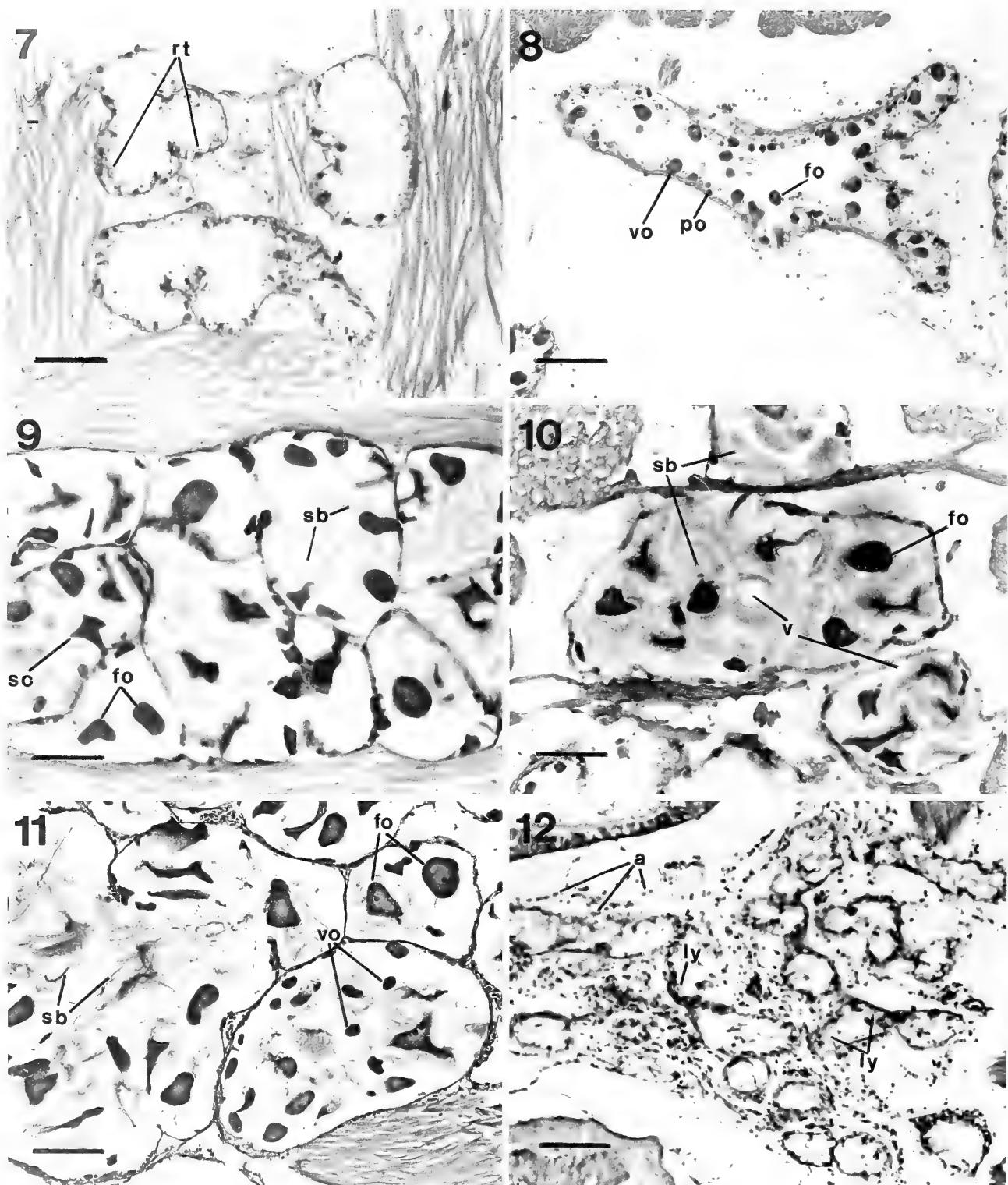
Maturity Scale in Females

Multiplication (Figure 7). Germ cells and abundant oogonia located in the reticulum of follicular cells (rt) form an inner annulus contiguous with the alveolar wall. There are also previtellogenic oocytes present. The fibers and cells as a whole confer a well defined aspect to the alveolar wall. The alveoli show irregular outlines and are dispersed, occupying 20 to 40% of the available inter-alveolar space. The lumen is spacious and generally represents more than 80% of the intra-alveolar space.

Early Maturation (Figure 8). Vitellogenic oocytes (vo) less than 20 μ m in diameter are adherent to the acini walls, displaying rounded shapes. There is no material among these cells; oogonia and previtellogenic oocytes

(po) are abundant. Alveoli are rounded, occupying a percentage of the lumen similar to that of the preceding stage.

Advanced Maturation (Figure 9). Vitellogenic oocytes reach maximum diameters of 50 μ m and become flattened, oval, or lobulated. Some of the cells, still attached to the alveolar walls, take stalked shapes (so). The basophilic substance (sb), contiguous with the vitellogenic oocytes' plasmatic membrane, is clearly visible, occupying most of the internal space of the alveoli. Oogonia and previtellogenic oocytes are abundant. Alveoli spread over 40 to 80% of the available space, in some cases deforming the adjacent muscular packs and imprinting irregular shapes on the neighboring digestive diverticula.



Figures 7-12. Appearance of the female gonads at different maturity stages. Figure 7. Multiplication. Figure 8. Early maturation. Figure 9. Advanced maturation. Figure 10. Maximum maturation with partial spawn. Figure 11. Spawning. Figure 12. Regression. Key: a, amoebocyte; fo, free oocyte; ly, lymphocyte; po, previtelogenic oocyte; rt, reticular tissue; sb, basophilic substance; so, stalked oocyte; v, vacuity; vo, vitellogenic oocyte. Scale bars = 100 μm .

Maximum Maturation with Partial Spawn (Figure 10). Free oocytes (fo) reach maximum diameters and take compressed shapes. The basophilic substance (sb) around them shows well defined limits. It is possible to distinguish empty spaces (v) similar in shape and size to those of the cells remaining free in the lumen, suggesting that some of them have been evacuated. It is also possible to observe abundant oogonia, previtellogenic oocytes, and stalked oocytes. Alveoli spread over more than 80% of the available space and present polyhedral shapes due to the dense packing.

Spawning (Figure 11). The intra-alveolar space is ample, and some free oocytes (fo) still remain in it. Several vitellogenic cells (vo) of submaximal size ($d < 20 \mu\text{m}$) are free in the lumen, suggesting a massive detachment from the alveolar walls. Oogonia and previtellogenic oocytes are scarce. The alveoli recover rounded outlines, with a lobulated aspect in some cases, and lose contact with the adjacent organs and tissues.

Regression (Figure 12). Free oocytes have been fully evacuated; there are follicular cells in the lumen, and oogonia and oocytes among them. Eosinophil amoebocytes (a) are abundant, and lymphocytes (ly) appear grouped around the oocytes remaining in the wall. The alveoli occupy approximately 20% of the available space, dispersed among the other tissues, and appear flattened.

Maturity Scale in Males

Multiplication (Figure 13). There are primary germ cells in the alveolar walls. The most abundant cells are the spermatogonia (sg), especially among the follicular cells of the inner portion of the alveoli. In addition, there are several phagocytic cells (a) remaining from the inactivity phase (gonadal regression). The alveoli are irregular or rounded, abundant, small in diameter, and occupy 20 to 40% of the available space.

Early Maturation (Figure 14). The alveoli are filled with primary and secondary spermatocytes (sc), which appear grouped in dense packets among the spaces delimited by the follicular cells. At the periphery of the spermatocytes there are abundant spermatogonia. Spermatids and spermatozoa appear in some alveoli. The alveoli are rounded and have a greater diameter than those of the preceding stage, occupying 40 to 60% of the available space among the adjacent tissues.

Advanced Maturation (Figure 15). Dense cell masses detached from the alveolar walls fill the alveoli, occupying around 80% of the inner space. Spermatids and spermatozoa are abundant in all the alveoli, but they do not usually fill more than 40% of the space occupied by the cells of the entire spermatocytic series. Spermatocytes occupy the highest proportion of space within the alveoli. The spermatozoa (sz) appear in dense lines, in contact with septa of deep eosinophil conjunctive fibers (ef, Figures 6,15) formed at the inside of the alveoli. The recip-

rocal compression among alveoli produces a honeycomb pattern. The space occupied by the alveoli is 60 to 90% of the total.

Partial Evacuation with Recuperation (Figure 16). Spermatozoa present in the former stage have been evacuated. It is possible to observe several rounded and well defined vacuities among the cell mass (v). There are fewer spermatozoa than in the former stage, but it is possible to observe a dense mass of spermatocytes and spermatogonia. Other aspects are similar to those of the "advanced maturation" stage.

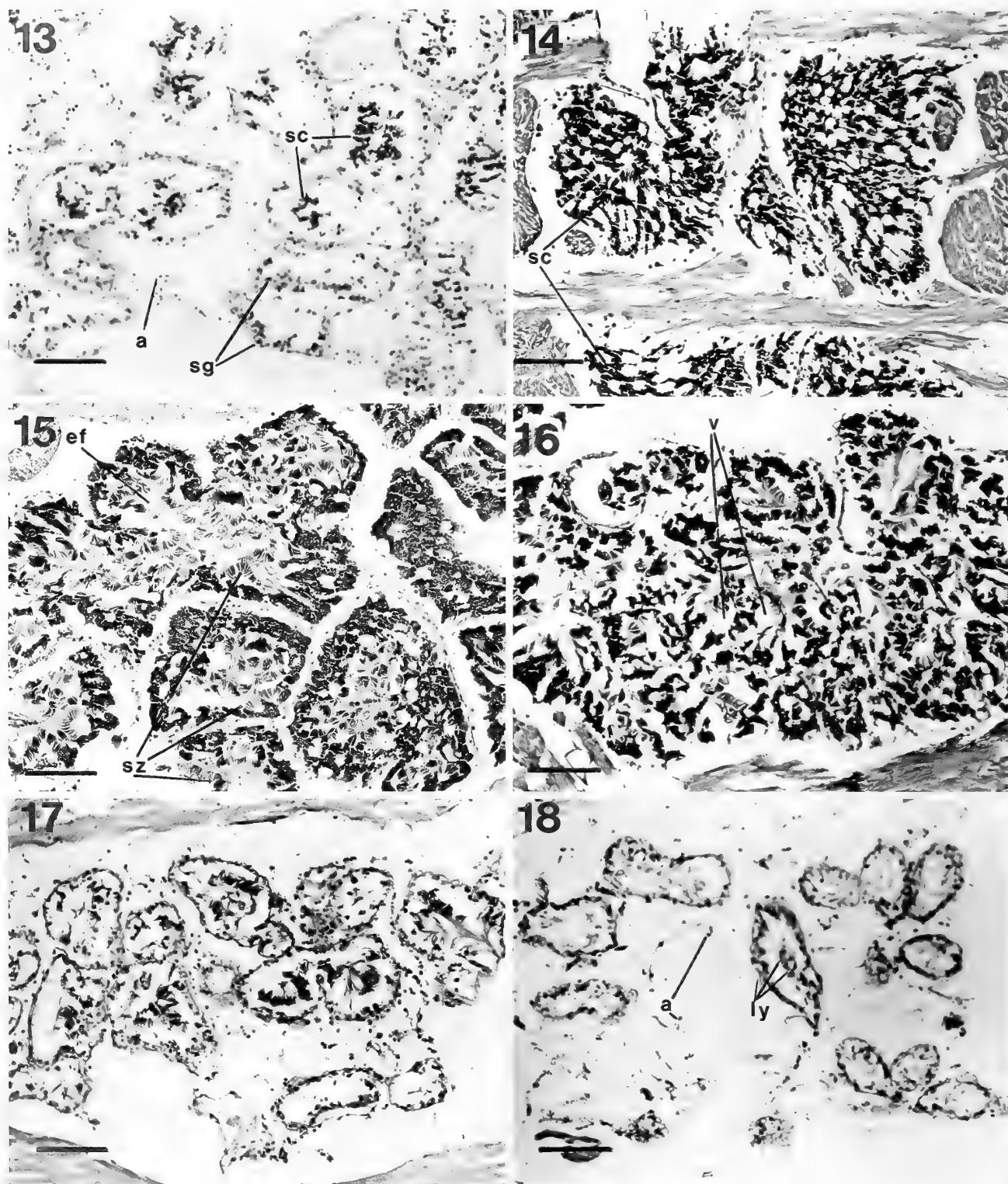
Evacuation (Figure 17). Spermatozoa, spermatids, and spermatocytes have nearly all been evacuated. The reticulum of follicular cells becomes more dispersed. A few remaining spermatogonia and spermatocytes appear attached to the alveolar walls. The alveoli are rounded, and the space among them has increased. The space occupied by the alveoli is 20 to 40% of the total.

Regression (Figure 18). The alveoli are nearly empty; it is not possible to observe spermatozoa or spermatids. There are abundant amoebocytes (a) and lymphocytes (ly) around the remaining spermatocytes and spermatogonia. The reticulum of follicular cells is absent or very scarce. The alveoli appear reduced in diameter and dispersed, occupying less than 20% of the available space.

Seasonal Variation of Gonadal Stages

In females (Figure 19), the multiplication began in June, and this stage was proportionally the most abundant in the winter samples. Between August and November, early maturation becomes advanced maturation. First partial spawnings were registered in November. Maximum maturation with partial spawning was the most abundant stage between November and February, but was scarce in March. Toward late summer and early autumn, female gonads were in regression, a stage that remained dominant until the beginning of the next winter.

In males (Figure 19), multiplication began in May and finished in September. Though the multiplication was, as in the females, the most abundant stage in winter, it was also possible to find males in early maturity after June. Early maturation was the most abundant stage toward late winter and early spring, whereas advanced maturation was the dominant stage during the spring months. First partial evacuation occurred in December, slightly later than the first partial spawning of the females. From December to February, most of the clams were in partial evacuation with recuperation stage. During the same period, it was still possible to find a considerable proportion of male gonads in advanced maturation. Final evacuation was detected in February and March, with a few delaying until April. Gonadal regression was initially detected in March; this stage was dominant in April and May, and it decreased gradually from June to August.



Figures 13–18. Appearance of the male gonads at different maturity stages. Figure 13. Multiplication. Figure 14. Early maturation. Figure 15. Advanced maturation. Figure 16. Partial evacuation with recuperation. Figure 17. Evacuation. Figure 18. Regression. Key: a, amoebocyte; ef, eosinophil fibers; ly, lymphocyte; sc, spermatocyte; sg, spermatogonia; sz, spermatozoa; v, vacuity. Scale bars = 100 μ m.

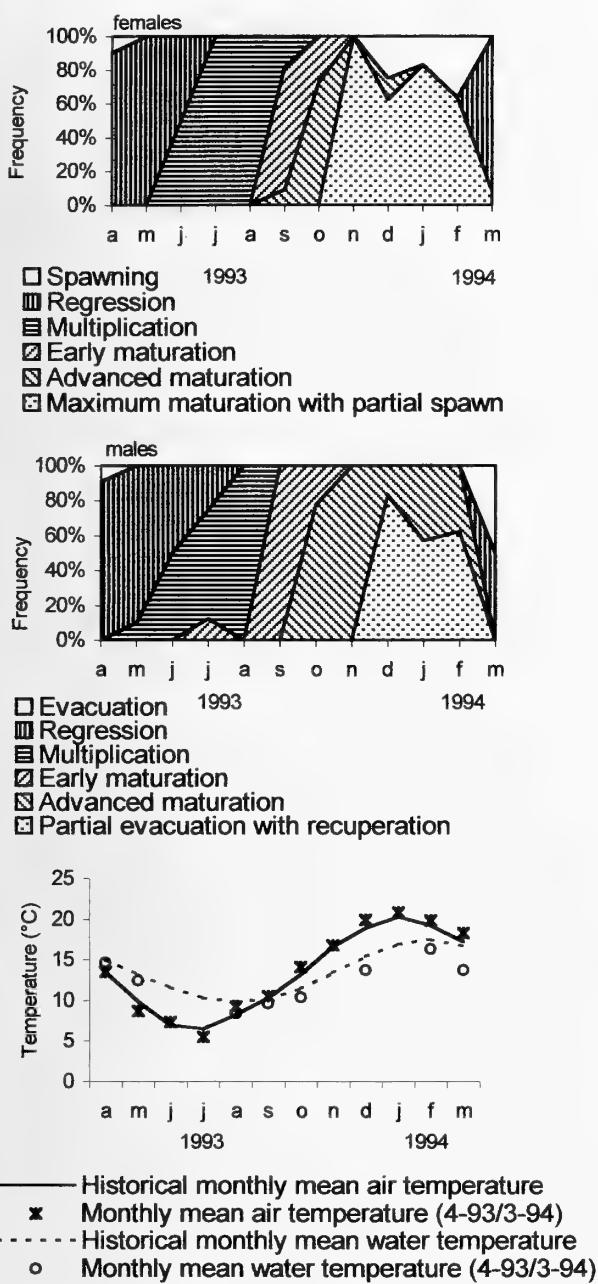


Figure 19. Percentage variations of occurrence of different gonadal stages by month, and monthly mean air and surface water temperature registers. Top: females; center: males; bottom: temperatures.

Seasonal Variation of the Percentage of Alveolar Area (PAA)

In females, PAA ranged between 13.9% (April) and 85.4% (December) (Figure 20). A gradual increase was detected during autumn and winter, except in September when the PAA was relatively low. After October, the PAA increased conspicuously until it stabilized at a maximum

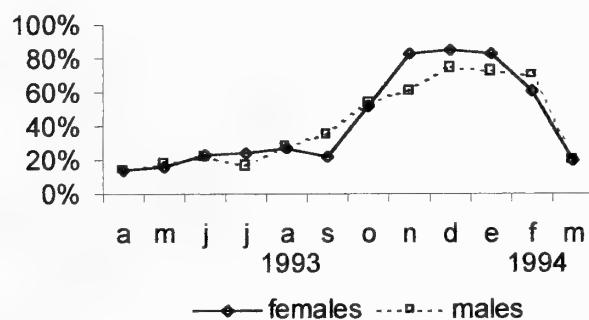


Figure 20. Monthly averages of the percentage of alveolar area (PAA) for both sexes.

from November to January. In February and March, the average PAA values decreased significantly.

In the males the lowest PAA average was observed in April (14.1%). After that, it increased gradually until December (80.4%) (Figure 20). During the subsequent months, higher values of PAA were detected. March was characterized by a conspicuous decrease in PAA.

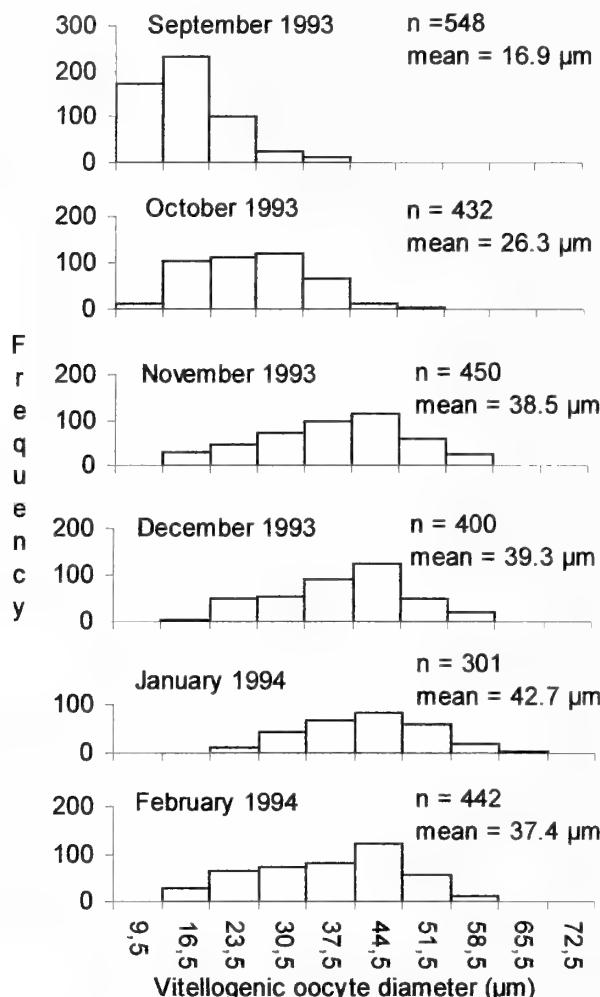
Frequency Distribution of Vitellogenetic Oocytes Diameter

Vitellogenetic oocytes were present in the gonads of all females from September until February. Analysis of vitellogenetic oocyte size frequency distribution by month shows the lowest values in September (6–39 µm, average = 17 µm), an important increase in October and November, and stabilization in December and January. Highest oocyte diameters were observed in January (16–71 µm, average = 43 µm), while a slight decrease was detected in February (Figure 21). In March, vitellogenetic oocytes were only present in a small percentage of females (12.5%) due to full evacuation or reabsorption. A high correlation between average oocyte diameter per individual and the square root of the corresponding mean PAA was detected ($r = 0.90$, $n = 52$).

DISCUSSION

It has been reported that occasional hermaphroditic individuals occur in several species of bivalves defined as dioecious (Coe, 1945). However, this pattern is not frequent in Tellinidae (Lammens, 1967; Rae, 1978; Salzwedell, 1979; Brousseau, 1987; Kawai et al., 1993). Furthermore, individuals of *T. petitiana* with both sexes were not detected during this study.

Sex ratio in *T. petitiana* is not different from the 1:1 relationship reported for other tellinids and strict gonochoric bivalves such as *Macoma secta* and *Macoma nasuta* (Rae, 1978); *Tellina fabula* (Salzwedell, 1979); *Donax gouldii* Dall, 1921 (Fretter & Graham, 1964); *Mulinia lateralis* (Say, 1822) (Calabresse, 1969); *Spisula solidissima* Jones, 1981); *Protothaca asperrima* (Palacios et al.,



coincided with cytoplasmatic enlargement sizes due to advanced maturation. The males showed a similar pattern, with a very prominent PAA increase during October and November (advanced maturation), a decrease from January to April (evacuation with partial recuperation and evacuation stages), lower values in April and May (regression), and a moderate increase between May and August (multiplication). Variation and range of indexes similar to those of the PAA reported here for *T. petitiana* have been found in other bivalves. The proportion of the visual field occupied by gonad tissue in *Spisula solidissima* males ranged from 9.1–66.5% to 26.5–77.5% in 2 consecutive years (Kanti et al., 1993). In *A. tehuelchus* the female alveolar area increased from 30% to 97% between July and December, while the same variable represented about 40% during March–June (Lasta & Calvo, 1978).

There is a high correlation between the average diameters of vitellogenic oocytes per individual and the square roots of the corresponding PAA. In agreement with this, oocyte size matches the gonadal stage sequence detected in *T. petitiana*. The smallest average vitellogenic oocyte diameter agrees with early maturation stage found during September and advanced maturity of October. The larger oocytes observed between November and January are typical of the maximum maturation with partial spawn. The decrease in February coincides with the spawning registered in a large proportion of clams. The massive spawning detected between February and March is shown by the absence of vitellogenic oocytes from 87.5% of the individuals analyzed in the last month.

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Three New Records of Indo-West Pacific Littorinidae (Gastropoda) in the Tropical Eastern Pacific

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Abstract. Three species of Littorinidae that are widespread in the Indo-West Pacific (IWP) region are recorded from the Tropical Eastern Pacific (TEP) for the first time: *Littoraria undulata* (Gray, 1839) on Isla del Coco, *L. coccinea* (Gmelin, 1791) on Isla del Coco and Clipperton Atoll, and *Peasiella conoidalis* (Pease, 1868) on the mainland of Costa Rica. These are briefly described and figured. It is suggested that these may have been transported to the TEP as pelagic eggs or larvae, carried on the North Equatorial Countercurrent, perhaps during the enhanced flow characteristic of El Niño events. Records of IWP mollusks in the TEP are reviewed and reasons for the general lack of established populations of these species are discussed.

INTRODUCTION

The marine zoogeographic region of the Tropical Eastern Pacific (TEP) is separated from that of the Indo-West Pacific (IWP) by more than 5000 km of open ocean. Lacking islands as stepping stones, this expanse of deep ocean provides an obstacle to the trans-Pacific dispersal of shallow-water organisms and has been termed the “Eastern Pacific Barrier” (EPB; Ekman, 1953). The EPB is widely acknowledged as the most effective marine barrier to the dispersal of tropical shelf invertebrates in the modern oceans and throughout the Cenozoic (Grigg & Hey, 1992). Nevertheless, there is increasing evidence that the EPB is by no means impassable and that it in fact acts more as a filter bridge than a barrier, since some species are found on both sides. Compilations of these trans-Pacific distributions have been made for various animal groups including corals (Glynn & Ault, 2000), echinoderms (Lessios, et al., 1996), shorefishes (Robertson & Allen, 1996), and mollusks (Emerson, 1991; Emerson & Chaney, 1995). In nearly all of these cases, the TEP records have been explained by relatively recent dispersal from the IWP to the east; only in the case of a few shorefishes are there clear examples of TEP endemics that have crossed the barrier in the reverse direction (Robertson & Allen, 1996). An alternative interpretation is that trans-Pacific distributions are of more ancient origin, representing relicts of previously continuous Tethyan distri-

butions that were separated by vicariance as the EPB developed (McCoy & Heck, 1976; Heck & McCoy, 1978; Rowe, 1985). For a small number of invertebrate species there is now molecular evidence to support the dispersalist interpretation that disjunct populations of trans-Pacific species have indeed been connected by recent gene flow, and are not ancient isolates (Lessios, et al., 1998).

The causes of the apparent asymmetry of dispersal of tropical shallow-water invertebrates across the EPB are debated and may involve both current patterns and ecological factors (Scheltema, 1988; Grigg & Hey, 1992). Currents that are believed to transport larvae and propagules across the Pacific flow in both directions, but show seasonal variation in intensity and composition, so that prediction of their influence on dispersal is difficult. Those flowing westward are the North Equatorial and South Equatorial Currents, originating in the temperate Californian and Peruvian biogeographic provinces respectively; it has been claimed that these are too cool to be vehicles for tropical Panamic species (Zinsmeister & Emerson, 1979), but they do in fact contain a component of tropical water (Scheltema, 1988). The major warm-water currents traversing the EPB flow along and north of the Equator in an eastward direction, the North Equatorial Countercurrent (NECC) and cooler subsurface Equatorial Undercurrent. The source area for IWP immigrants to the TEP is generally considered to be the Line Islands, since the most direct route across the EPB is the 5400 km from Christmas Island to Clipperton Atoll in the path of the eastward flowing NECC (Richmond, 1990; Finet, 1991; Grigg & Hey, 1992). This is a seasonal cur-

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rent, flowing from May to December, and during normal years the time taken to cross the EPB has been estimated at a mean of 155 days, or as little as 100 days (Richmond, 1990). However, this time may be reduced to only 50–60 days during periodic El Niño-Southern Oscillation (ENSO) events, when the rate of eastward surface flow and latitudinal extent of the current are increased (Richmond, 1990; Glynn et al., 1996). ENSO events occur every four to nine years, with unusually strong episodes once or twice in a century (Grigg & Hey, 1992). Although few long-term records are available, it has been noticed that new and infrequent records of IWP species in the TEP frequently coincide with or immediately follow strong ENSO events (Kay, 1991; Emerson & Chaney, 1995; Lessios et al., 1996, 1998; Robertson & Allen, 1996).

Mollusks provide especially clear examples of trans-Pacific migrants and the influence of ENSO events, since they are thoroughly collected, geographical ranges are relatively precisely known, life histories are often understood, and larvae have been recorded in oceanic currents. The gastropod species of IWP origin that have been recorded in the TEP have been reviewed most recently by Emerson (1991) and the Cypraeidae by Emerson & Chaney (1995). In addition to the references cited by these authors, further records have been added, and in some cases removed, by others (Shasky, 1983, 1986, 1987a,b, 1988, 1995; Kay, 1991; Emerson, 1993, 1994, 1995, 1999; Chaney, 1996; Hollmann, 1996; Kaiser, 1997, 1998, 1999; Hertz & Kaiser, 1998; Reid, 1999a). Those presumed to be of natural occurrence (rather than human introduction) consist of 77 species (excluding cases recognized as subspecifically distinct). Of these trans-Pacific taxa, 14 are tonnoideans, many of which have distributions throughout the worldwide tropics and are known to be widely dispersed by means of exceptionally long lived teleplanic larvae (Scheltema, 1988). The remainder are mostly members of the Cypraeidae (12 species, Emerson & Chaney, 1995) and Neogastropoda (32 species). Of the non-tonnoideans the great majority represent rare occurrences rather than established populations, and about 60% of them are recorded only from the islands of the TEP and not from the American mainland (Emerson, 1991). Of the few that maintain viable, self-sustaining populations in the TEP, two are considered sufficiently distinct morphologically from IWP populations that they are accorded the status of subspecies (Vermeij, 1990; Reid, 1999a). Three additional species have been interpreted as TEP endemic species with a recent ancestry in the IWP (Vermeij, 1990).

The family Littorinidae is one of the most thoroughly studied among marine gastropods; its taxonomy is largely resolved, and both distribution and larval development are known for most species (e.g., Rosewater, 1970; Reid, 1986, 1989a,b, 1999a; Reid & Mak, 1998). The littorinid fauna of the TEP (from the Gulf of California to north-

ernmost Peru) is being revised and is presently known to consist of six species of *Littoraria* (Reid, 1999a), 15 of *Nodilittorina* (Reid, in preparation), and a species introduced from the western Atlantic (*Cenchritis muricatus* [Linnaeus, 1758]; Bishop, 1992; Chaney, 1992). Of these species, only one, *Littoraria pintado* (Wood, 1828), is known to have a trans-Pacific distribution, and the populations in the TEP are classified as an endemic subspecies, *L. pintado pullata* (Carpenter, 1864) on account of their consistently darker shells (Reid, 1999a). Among trans-Pacific gastropods this species is unusual in several respects. The TEP populations are restricted to Isla del Coco (Cocos Island), Clipperton Atoll, the Revillagigedo Islands, southern Baja California, and a few isolated occurrences on the southern mainland of Mexico. At least on the islands and in Baja California, the populations are large, clearly self sustaining, and not dependent upon immigration from the IWP. (To these records can be added a single live-collected specimen of *L. pintado pullata* from the Isla de Malpelo, Colombia; leg. K. L. Kaiser, 30 March 1998; K. L. Kaiser Collection.) Reid (1999a) argued that since the closest IWP occurrences are in the Hawaiian Islands, rather than in the traditional source area of the Line Islands, it is likely that there is at present no genetic contact between the two subspecies, even during exceptional ENSO events. There is one other record of an IWP *Littoraria* in the TEP, based on a single shell of *L. intermedia* (Philippi, 1846) from the Galápagos Islands (Wreck Bay, Chatham Island, 1937, G. Vanderbilt Collection, ANSP 170348; Reid, 1986). This occurrence has not been confirmed and is considered unreliable; Reid (1986) regarded the record as doubtful (see also remarks in Systematic Descriptions below on an unreliable collection of *Littoraria coccinea* from the same source).

In the course of the study of the littorinids of the eastern Pacific, three IWP littorinids new to the fauna of the TEP have been found and are recorded here.

MATERIALS AND METHODS

Approximately 1000 lots of littorinids from the TEP have been examined, including both personal collections and material in major museums (Natural History Museum, London, BMNH; National Museum of Natural History, Washington, D.C., USNM; Natural History Museum of Los Angeles County, LACM; Muséum National d'Histoire Naturelle, Paris, MNHN; additional material from the Academy of Natural Sciences of Philadelphia, ANSP; Museum of Comparative Zoology, Harvard; California Academy of Sciences, CAS; Santa Barbara Museum of Natural History, SBMNH). In addition, the faunistic literature on the TEP has been thoroughly checked. In the following descriptions only brief synonymies are given, indicating references to recent taxonomic accounts.

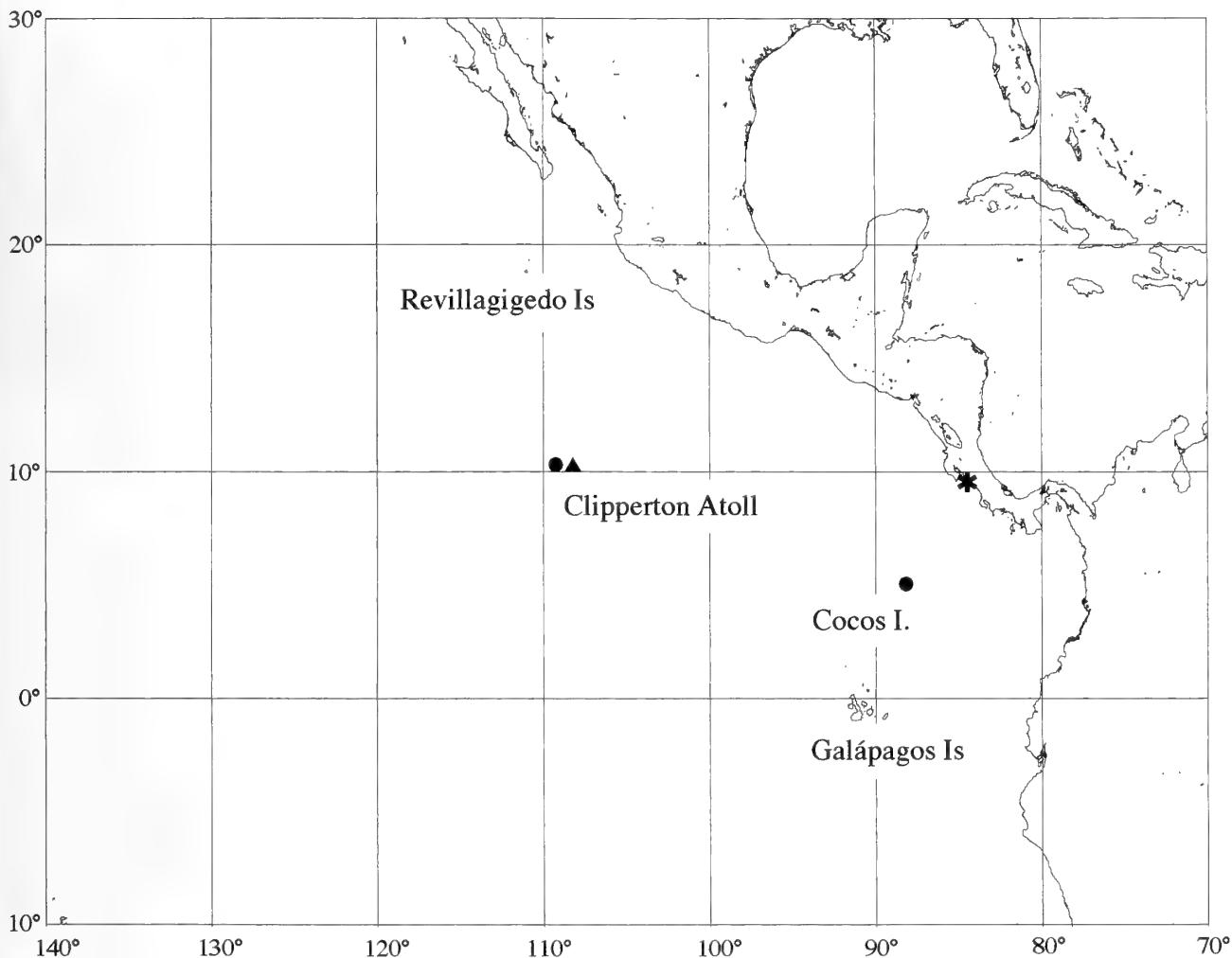


Figure 1. Map of new records of Indo-West Pacific Littorinidae in tropical eastern Pacific: *Littoraria undulata* (triangle), *L. coccinea* (circles), and *Peasiella conoidalis* (asterisk).

SYSTEMATIC DESCRIPTIONS

Littoraria (Protolittoraria) undulata (Gray, 1839)

(Figure 2A)

Littorina undulata Gray, 1839:140 (lectotype BMNH 1968362; Okinawa, Ryukyu Islands; lectotype and type locality designated by Rosewater, 1970).

Littorina (Littoraria) undulata Rosewater, 1970:436–439 (includes synonymy), pl. 325, figs. 8–10, pl. 332, pl. 333 (radula, penis, egg capsule).

Littoraria (Littoraria) undulata Reid, 1986:73, figs. 4e (penis), 99 a–c. Reid, 1992:195, figs. 1d (penis), 2d (oviduct), pl. 4c, d.

Littoraria undulata Reid & Mak, 1999:figs. 3G, H (radula). *Littoraria (Protolittoraria) undulata* Reid, 1999b:310.

Diagnosis: Shell height to 26 mm, solid, height/breadth ratio = 1.45–1.71; columella long, straight, wide; sculpture of 7–10 primary grooves on spire whorls, increasing

to 22–36 (rarely to 53) incised lines on last whorl, but sculpture sometimes faint; color variable, whitish, grey or pink, with spots, axial streaks or marbled pattern of dark or red brown, often forming 8–14 zigzag or axial lines on last whorl, columella lilac. Penis with bifurcate base, short filament less than half length of wrinkled base, sperm groove open; very large glandular disc. Pallial oviduct a single spiral of albumen and capsule glands, 5.5 whorls. (After Reid, 1992.)

Record in TEP (Figure 1): One live specimen, Bahía Wafer, Isla del Coco, Costa Rica, 26 May 1985, leg. K.L. Kaiser, SBMNH 345468 (Figure 2A).

Remarks: This species occurs on a range of substrates in the littoral fringe, including basalt, limestone, beach-rock, concrete, driftwood, and (rarely) mangroves, both on oceanic islands and continental shores (although it is absent in turbid situations). It is one of the most wide-

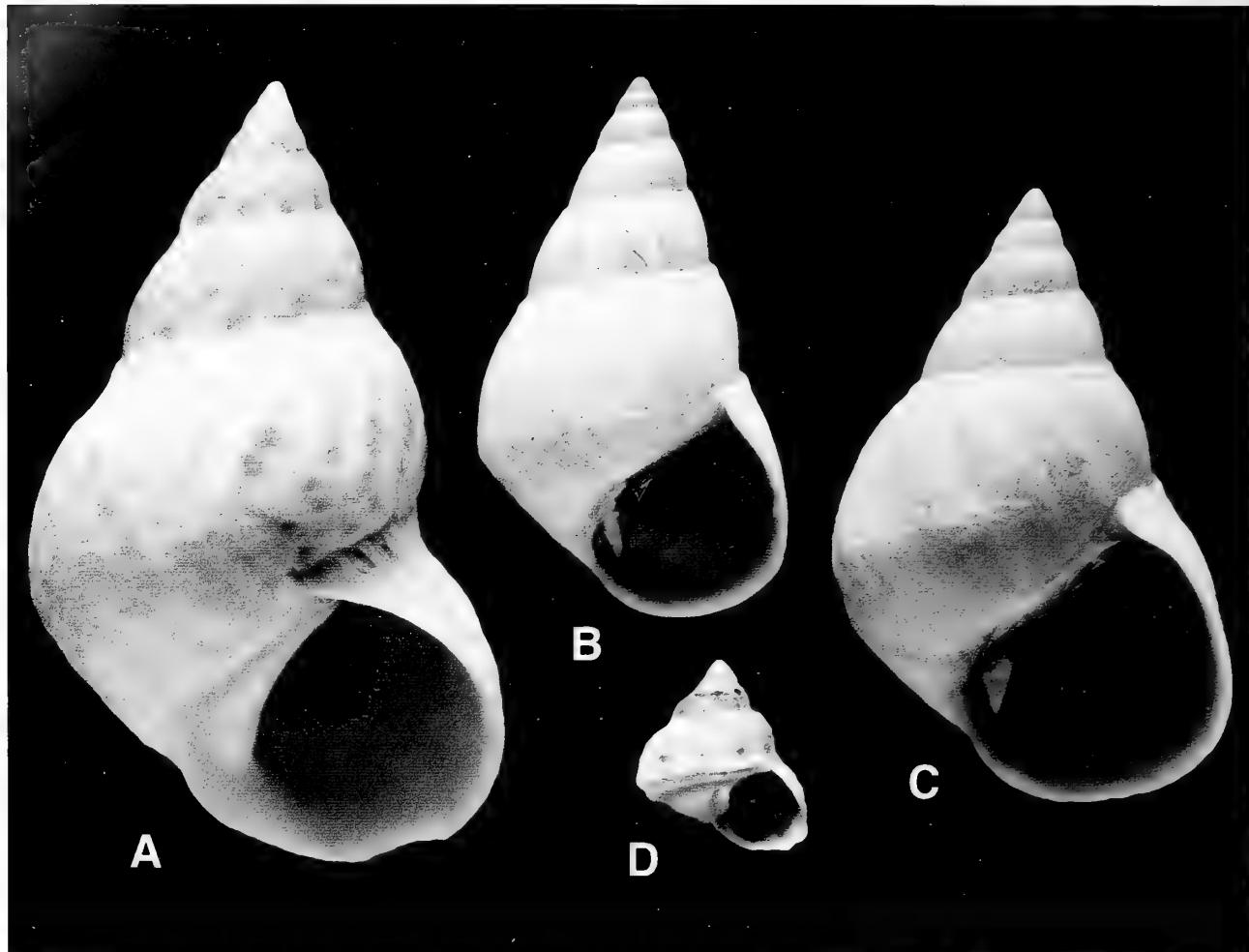


Figure 2. Shells of Indo-West Pacific Littorinidae newly recorded in the Tropical Eastern Pacific. A. *Littoraria undulata* (23.7 mm; Bahía Wafer, Isla del Coco, Costa Rica; SBMNH 345468). B. *Littoraria coccinea* (16.1 mm; SE corner Clipperton Atoll; SBMNH 345467). C. *Littoraria coccinea* (19.3 mm; Bahía Chatham, Isla del Coco, Costa Rica; SBMNH 345466). D. *Peasiella conoidalis* (1.1 mm diameter; off Bahía Herradura, Puntarenas Province, Costa Rica; LACM 72-54).

spread of IWP littorinids, from South Africa (Kilburn, 1972), India, Indonesia, Australia, and all across the western Pacific to Hawaii and Palmyra in the Line Islands (Rosewater, 1970: pl. 334), including Hong Kong (Reid, 1992), but excluding Polynesia. The pelagic egg capsule has been described (Rosewater, 1970: pl. 333, figs. C, D), and like all but one of its congeners it undoubtedly undergoes planktotrophic development (Reid, 1989a).

In shape, the shell shows some similarity to that of *Littoraria pintado pullata* (see Reid, 1999a), but in that species the coloration is blackish or dark brown, with a pattern of dense dots or spiral lines, and the columella is white edged with brown. Also similar is the shell of *L. rosewateri* Reid, 1999 (see Reid, 1999a: figs. 9A–D), but with a smaller, taller shell and a short columella; that species is restricted to mangrove, salt marsh, and muddy habitats on mainland shores from Mexico to Ecuador. The

shell of *L. undulata* is distinguished from that of the other rare IWP immigrant *L. coccinea* by its stronger sculpture, long lilac columella, and brown pattern; penial shapes are also diagnostic.

Littoraria (Protolittoraria) coccinea (Gmelin, 1791)

(Figures 2B, C)

Helix coccinea Gmelin, 1791:3651 (lectotype figure Martyn Universal Conchologist vol. 2, pl. 68, left external figure; Tahiti; lectotype and type locality designated by Rosewater, 1970).

Littorina (Littoraria) coccinea Rosewater, 1970:439–441 (includes synonymy), pl. 325, figs. 11, 12, pl. 335, pl. 336 (radula, penis, egg capsule).

Littoraria (Littoraria) coccinea Reid, 1986:73, fig. 4b (penis).

Littoraria coccinea Reid & Mak, 1999: figs. 3A, B (radula).

Littoraria (Protolittoraria) coccinea Reid, 1999b:310, fig. 1H (egg capsule).

Diagnosis: Shell height to 29 mm, solid, height/breadth ratio = 1.40–1.64; columella short; sculpture of 8–10 primary grooves on spire whorls, usually becoming obsolete on last whorl leaving a smooth glossy surface; color whitish, with pink peripheral band, darker on spire whorls, pink growth lines on last whorl, columella and aperture dark orange, columella usually tinged with purplish brown. Penis with bifurcate base, long vermiform filament two to three times length of wrinkled base, sperm groove open; moderately large glandular disc. Pallial oviduct a single spiral of albumen and capsule glands, 5.5 whorls.

Records in TEP (Figure 1): Three live specimens, Bahía Chatham, Isla del Coco, Costa Rica, 23 May 1985, leg. K.L. Kaiser, SBMNH 345466 (Figure 2C); one live specimen, SE corner Clipperton Atoll, 28 April 1998, leg. K.L. Kaiser, SBMNH 345467 (Figure 2B). One lot of 16 specimens from Wreck Bay, Chatham Island, Galápagos Islands (leg. R.W. Smith, 1931, G. Vanderbilt Collection, ANSP 170347) is considered unreliable. This is because the sample is remarkably large for a rare immigrant species. Furthermore, the following lot in the ANSP registration sequence is a shell of another IWP species, *Littoraria intermedia*, said to be from the same locality (see Introduction above). This coincidence is likely the result of mislabelling.

Remarks: This species is likewise found on a range of substrates in the littoral fringe, including basalt, concrete, limestone, and driftwood, but is restricted to islands and shores with clear oceanic water. It is largely confined to the western Pacific, from the Ryukyu Islands and the Philippines across Oceania to Hawaii, the Line Islands and Polynesia, and including islands of the Australian Barrier Reef (Rosewater, 1970: pl. 337). There is one record from the Cocos-Keeling Islands in the Indian Ocean (Rosewater, 1970; DGR personal observation of USNM 589143); here, as elsewhere in the Indian Ocean, the more common species is *L. glabrata* (Philippi, 1846), sister species of *L. coccinea*. The egg capsule has been figured by Rosewater (1970) and Reid (1999b), and the species undoubtedly undergoes planktotrophic development (Reid, 1989a).

Its smooth, pinkish-white, orange-mouthed shell is highly distinctive and should not be confused with that of any other species in the TEP. The lack of dark color pattern, short columella without lilac color, and virtually smooth shell distinguish this species from the other IWP immigrant, *L. undulata*.

Peasiella conoidalis (Pease, 1868)

(Figure 2D)

Trochus conoidalis Pease, 1868:287, pl. 24, fig. 8 (4 syn-types ANSP 18868; Paumotus [= Tuamotu Islands]).

Peasiella conoidalis Reid, 1989b:55–56 (includes synonymy), figs. 2, 16, 18 (protoconch), 23–24 (radula), 37–38 (penis), 74–81. Reid & Mak, 1998:26–28, figs. 138–141.

Diagnosis: Shell to 5 mm diameter, trochoidal, height/breadth ratio = 0.77–1.33; periphery strongly keeled with a straight or crenulated flange; small open umbilicus; sculpture of 4–12 grooves above periphery, 4–8 ribs on base; color white to yellow with minute brown dots or lines in grooves. Operculum corneous, multispiral. Penis long, vermiform, with closed sperm groove; single mamilliform penial gland at half length of penis. Pallial oviduct a backward loop of albumen gland followed by larger loop of capsule gland; copulatory bursa absent. (After Reid, 1989b.)

Record in TEP (Figure 1): One dead specimen, 20 fathoms (37 m), off Bahía Herradura, Puntarenas Province, Costa Rica, 10 March 1972, leg. McLean & Bussing, RV *Searcher*; LACM 72–54 (Figure 2D).

Remarks: The habitat of this species is lower on the shore than that of the larger littorinids, and it can be found among coral rubble on intertidal reef flats and among barnacles on beachrock, mainly on atolls and oceanic islands (Reid, 1989b). The recorded shell was dead collected, and the depth of 37 m is well outside its known intertidal habitat. Its distribution is wide, stretching from Kenya to southern Japan, northeastern Australia and across the Pacific to the Line Islands and Polynesia (Reid, 1989b; Reid & Mak, 1998). All known species of *Peasiella* possess a large capsule gland in the pallial oviduct and a protoconch that indicates planktotrophic development (Reid, 1989a, b); the pelagic egg capsules of several species have been described (Reid & Mak, 1998).

This is the first record of the Indo-West Pacific genus *Peasiella* in the TEP. The generic name was used for a new species, *Peasiella roosevelti*, described from the Galápagos by Bartsch & Rehder (1939), but that has been shown to be a synonym of *Nodilittorina porcata* (Philippi, 1846) (Reid, 1989a). Confusion of this with other littorinid species in the TEP is unlikely; the only species with similarly small umbilicate shells are members of the *Nodilittorina porcata* complex, but in those the outline is globular or carinate, rather than trochoidal, and there is often a coarse black color pattern. It is, however, possible that specimens of *P. conoidalis* may be misidentified as members of the Trochidae, and in such cases may have been overlooked in museum collections.

DISCUSSION

We have reported the occurrence of three IWP littorinids in the TEP, *Littoraria undulata* on Isla del Coco, *L. coccinea* on Isla del Coco and Clipperton Atoll, and *Peasiella conoidalis* on the mainland of Costa Rica (Figure 1). The last of these is a minute species that might hith-

erto have been overlooked or misidentified, but the two *Littoraria* species are large, distinctive, and easily collected in their high intertidal habitat. Neither was listed from Clipperton Atoll by Emerson (1994) nor from Cocos Island by Montoya (1983). All these new records fit the typical profile of most of the known records of IWP non-tonnoidean gastropod species in the TEP (Emerson, 1991): the species are widespread in the IWP (including the Line Islands) and of rare occurrence in the TEP; they have planktotrophic development and therefore the potential for dispersal in ocean currents, and (with the exception of *P. conoidalis*) they have been discovered on the oceanic islands of the TEP in the path of the eastward-flowing North Equatorial Countercurrent. It has been suggested that transport of IWP species to the TEP is more likely during ENSO events (Richmond, 1990), so it is interesting that the collections of living *Littoraria* were made during or shortly after the strong ENSO events of 1982–1983 and 1997–1998 (precise growth rate data are not available for these species, but in the case of the 1985 collections survival for 2–3 years is possible).

The means of transport of these species to the TEP can only be a matter of speculation. There is no doubt that all have pelagic eggs and planktotrophic development, but the length of larval life is unknown. The only tropical littorinid to have been successfully reared to metamorphosis is *Nodilittorina hawaiiensis* Rosewater & Kadolsky, 1981, which settled 3–4 weeks from spawning (Struhsaker & Costlow, 1968, as *Littorina picta*). A similar length of pelagic life can be predicted for the present species on the basis of similarity of egg size and protoconch. This length of time is still much less than the minimum estimate of 50–60 days to cross from the Line Islands to Clipperton Atoll in the NECC during peak flow at a time of an ENSO event (Richmond, 1990; Glynn et al., 1996). Still faster transport may be possible, as suggested by settlement in the TEP of the IWP coral *Acropora* with a larval competency period of less than 25 days (Richmond, 1990). It is also possible that larval competency of these littorinids can be extended in the absence of a suitable substrate for settlement, as shown by observations on the temperate *Littorina littorea* by Thorson (1946). It is notable that both *Littoraria* species occur frequently on driftwood on the shore, so that rafting of adults is another potential means of transport (Jokiel, 1990; Ó Foighil, et al., 1999). However, human transport of the *Littoraria* species cannot be entirely ruled out. An example of apparent human introduction of a similarly large littorinid to the TEP is the record of a colony of the western Atlantic *Cenchritis muricatus* in the Gulf of California (Bishop, 1992; Chaney, 1992). For the minute *Peasiella conoidalis*, which was not collected alive or in its natural habitat, does not occur on driftwood, and was found on the American mainland rather than on the oceanic islands, the means of transport to the TEP (and indeed the validity of the record) are still less clear.

One puzzling aspect of the increasingly numerous reports of IWP species appearing in the TEP is that the immigrants seldom appear to become established as self-sustaining populations. Furthermore, those that do so apparently do not generally survive to become genetically differentiated (or specifically distinct) from their IWP ancestors, so that the evolutionary importance of trans-Pacific dispersal is limited (Vermeij, 1990). The reasons for the apparent failure of IWP species to become established are debated, and may include temporal instability of sea temperature due to ENSO events, limited availability of suitable habitat (especially of reefs and oceanic islands), and possible competition with the indigenous biota (Vermeij, 1990; Emerson, 1991; Glynn & Ault, 2000). The restriction of records of many IWP immigrant species to the islands of the TEP (and absence from the continental mainland) may further be explained by the prevailing westward-flowing currents between islands and mainland (Zinsmeister & Emerson, 1979). The difficulty of establishment faced by a planktotrophic species as a consequence of its type of development should also not be underestimated. As pointed out by Johannesson (1988), such species may disperse over long distances, but the density of recruits to a small founding population in the next generation is likely to be too low to sustain the population, since eggs and larvae will be swept away. Ironically, it may be that species without pelagic stages have a better chance of successful colonization since recruits remain close to their parents. However, oceanic islands can nevertheless support self-sustaining populations of planktotrophic species, since larvae can be retained in local circulation patterns (Scheltema et al., 1996).

In a discussion of the biogeography and classification of the only other trans-Pacific littorinid, *Littoraria pintado*, Reid (1999a) suggested that genetic contact between populations in the IWP and TEP was most unlikely and that their consistent difference in shell color might be evidence of genetic differentiation, thus justifying their classification as distinct subspecies. The present new records of likely natural transport across the EPB do not alter this conclusion. In contrast to the three species recorded here, *L. pintado* is not known to occur in the Line Islands and furthermore occurs as large self-sustaining populations on the TEP islands. The closest IWP populations of *L. pintado* occur in the Hawaiian Islands that lie in the weak westward-flowing North Equatorial Current; although this may transport some fish species from the TEP to Hawaii (Robertson & Allen, 1996) it has not been indicated as a route for trans-Pacific mollusks.

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Size Variability of Juvenile (0+ Yr) Bay Scallops *Argopecten irradians irradians* (Lamarck, 1819) at Eight Sites in Eastern Long Island, New York

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Abstract. Size frequency distributions of juvenile (0+ yr) bay scallops *Argopecten irradians irradians* were examined at eight sites in eastern Peconic Bays, Long Island, New York, USA, with the specific goal of quantifying the prevalence of small juveniles (≤ 20 mm at the end of the first growing season in December). Sampling was conducted with a diver-operated suction dredge between late December 1990–early April 1991 until ≥ 200 individuals were obtained at each site. The non-normal, negatively skewed size frequency distributions, as well as scallop densities (range: 5.6–21.5/m²), differed significantly between sites. Shell heights of the 1773 sampled scallops ranged from 7–61 mm; median sizes ranged from 44–52 mm. Small juveniles composed between 0–8.7% of the different populations. Comparative sampling at two of the sites in summer 1991 showed equal or significantly higher survival of small juveniles from winter to summer, relative to larger individuals. The high prevalence of small juveniles during some years, and evidence from the literature that many of these individuals survive to spawn in their second year, compared to the typical semelparous reproductive pattern, suggest that small juveniles may be important to the persistence of bay scallop populations in certain years.

INTRODUCTION

The bay scallop *Argopecten irradians* (Lamarck, 1819) is an important commercial and recreational species along the Atlantic and Gulf coasts of the United States. Bay scallops are hermaphroditic and generally regarded as semelparous, although Belding (1910) estimated that up to 20% of a given year class of the northern subspecies *A. i. irradians* may survive to spawn in two successive years if not removed by the fishery. Spawning of *A. i. irradians*, which is found naturally from Massachusetts to New Jersey (Abbott, 1974), primarily occurs between late May to early September (see review by Barber & Blake, 1991) but may occur as late as November (Tettelbach et al., 1999).

Following larval settlement, shell growth of *A. i. irradians* in natural populations usually averages ~ 10 mm/

month until first season growth ceases around late November/early December (Belding, 1910; Kelley & Gieg, 1981; Tettelbach, 1991). By this time, mean shell height (measured as a tangent from the umbo to the middle of the ventral margin) of these juveniles or “seed” (0+ yr) is typically 30–55 mm (Belding, 1910; Marshall, 1960, Kelley & Sisson, 1981; Stewart et al., 1981; Tettelbach, 1991).

Occurrence of “small” juvenile scallops toward the end of the first growing season, however, has been reported by several authors. Taylor & Capuzzo (1983) reported evidence of 1–5 mm juveniles in Falmouth, Massachusetts during early November 1979, while bay scallop juveniles as small as 3 mm have been reported in eastern Long Island, New York waters during December of several years (P. Wenczel, personal observation). Kelley & Sisson (1981) concluded that small juveniles predominate in certain populations around Nantucket, Massachusetts, and Kelley (1981) suggested that large scallop harvests in certain areas where no seed was seen the pre-

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vious fall may result from high numbers of small juveniles that go unnoticed. For the present study, small juveniles were defined as individuals ≤ 20 mm in shell height at the end of their first growing season. Assuming a 1–2 week larval period (Loosanoff & Davis, 1963; Tettelbach & Rhodes, 1981) and shell growth of 10 mm/month from the time of larval settlement until the end of November, a 20 mm scallop thus would represent an individual that was spawned in mid-late September (a "late" spawn).

The prevalence of small juvenile *A. i. irradians* and their significance to natural populations remains unclear, probably because the most common methods of sampling (scallop dredges and *in situ* counts by divers) almost certainly underestimate their abundance. The purpose of the present study was to examine the size variability of juvenile (0+ yr) bay scallops at eight different sites in eastern Long Island, New York, USA, using a diver-operated suction dredge, with the specific goal of quantifying the prevalence of small juveniles.

MATERIALS AND METHODS

Sampling of juvenile scallops was conducted between 21 December 1990–1 April 1991, when water temperatures ranged from 3.3–7.8°C. Shell growth of *A. i. irradians* is known to cease when water temperature drops below 45°F ($= 7.1^\circ\text{C}$) and commences in the spring when water temperature reaches 45–50°F (7.1 – 10°C) (Belding, 1910). Thus, the period between December–early May has typically been reported as the period when no increase in shell growth occurs (Belding, 1910; Helm, 1983; Tettelbach, 1991). In the present study, the size of all sampled seed is considered to be the size they reached at the end of their first growing season.

Scallop sampling was conducted at eight different sites in the Peconic Bay system in eastern Long Island (Figure 1). Sites were chosen on the basis of scallop density, presence of eelgrass, geographical separation, their historical importance as scallop harvest areas, and/or anecdotal knowledge of small or large (≥ 57 mm) juvenile occurrence (the latter are legal to harvest in New York waters). Sampling at each site was done following a preliminary visual inspection of the bottom by divers to determine if eelgrass *Zostera marina* was present and if scallop density appeared to be high enough to obtain 200 juveniles in a reasonable period of time. While the sampling thus does not represent a random cross-section of each of the eight sites, the selection process permitted us to sample as many geographically distinct sites as possible. Sampling was completed over a linear distance of ~ 150 m at each of six sites, while at Barcelona Neck (B) and East Shelter Island (ESI) this distance was ~ 250 – 300 m.

All sampling was conducted with a 160 gpm diver-operated suction dredge equipped with a 5 hp engine and a 5–6 mm mesh collection bag; the effective minimum

retention size of the bags was 7–8 mm. A total of 167 haphazardly placed 1-m² quadrats were sampled on 16 different days, at MLW depths ranging from 0.7–2.3 m (Table 1). Collection of ≥ 200 seed at a given site required between 1–3 days (Table 1). Preliminary sorting was done on deck, while screening and picking of smaller scallops were done in the lab. Individuals that lacked a clear-cut, raised annual growth ring (Belding, 1910; Marshall, 1960; Helm, 1983) were classified as juveniles. Shell height of all scallops was measured to the nearest mm with calipers.

Retention efficiency of the suction dredge was evaluated on 21 December 1990 through blind sampling trials using marked scallops. Of 115 planted scallops, ranging in height from 14–36 mm, 100% were recovered shortly after they were dispersed into 10 different 1-m² quadrats in the eelgrass bed at the East Marion site. During field sampling of natural populations, two byssally attached scallops (< 20 mm) that were observed by divers in quadrats were not recovered from the mesh sampling bag, probably because these scallops were not picked up by the dredge.

Eelgrass density was determined at each site via visual counts of shoots in each of 10 haphazardly placed 0.043-m² quadrats. Sampling was completed between 28 March–1 April 1991, although eelgrass shoots persisted through the winter. Eelgrass densities ranged from 353–835 shoots/m² (Table 1). A Kruskal-Wallis test (Computing Resource Center, 1992) showed significant differences between eelgrass densities at the eight sites ($\chi^2 = 31.3$, 7 df, $P \leq 0.0001$). Non-parametric multiple comparisons tests (Zar, 1984) were similar statistically, except the Alewife Creek and Sag Harbor sites had significantly higher ($P < 0.05$) eelgrass densities (range: 686–835 shoots/m²) than the West and East Shelter Island sites (range: 353–530 shoots/m²).

Sampling in July and August 1991 was conducted to determine whether differential mortality of small juvenile scallops had occurred since the winter sampling period. This was done by comparing the proportion of small juveniles present at a given site during the winter versus the proportion of adult scallops in the summer with annual growth rings that were 7–20 mm from the umbo. Large juveniles (> 57 mm) and adults with large rings were excluded from these analyses because in New York the former are legal to harvest in their first winter and thus are selectively removed. Summer 1991 sampling was only conducted at the Greenport and Sag Harbor sites due to: (1) drastic reductions in scallop densities and (2) the passage of Hurricane Bob through the area on 19 August 1991. The latter created extensive windrows of scallops at some sites and probably differential transport of small and larger juveniles.

RESULTS

Overall mean density of 0+ yr scallops during the winter 1990–91 sampling period was 10.62 scallops/m². Counts

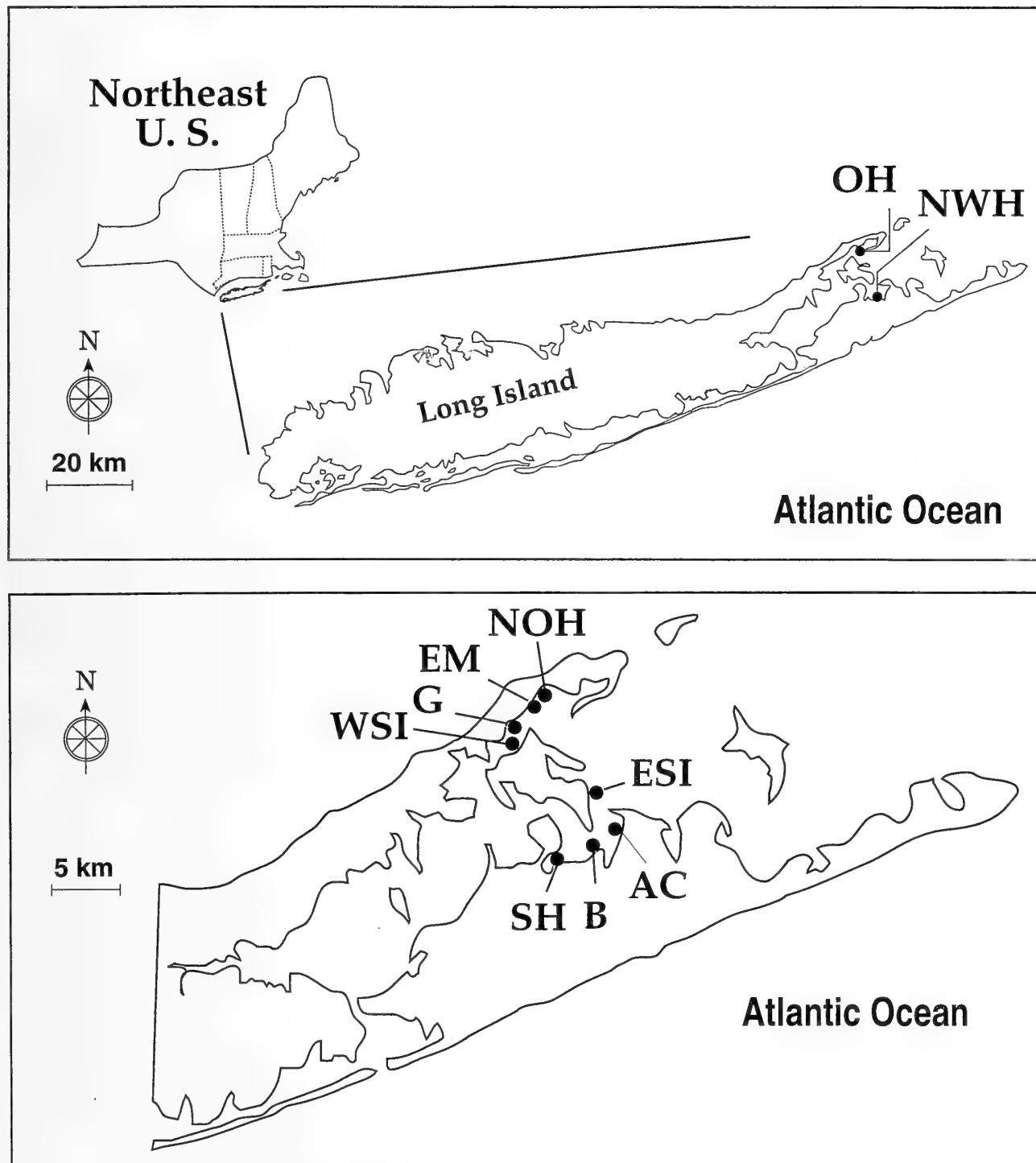


Figure 1. Maps showing location of Long Island, New York in the northeast United States, and location of sampling sites in the Peconic Bay system in eastern Long Island. OH = Orient Harbor, NWH = Northwest Harbor. See Table 1 for sample site abbreviations.

Table 1

Summary of sampling activities and parameters of the eight sites in eastern Peconic Bays, Long Island, New York, USA at which bay scallop size frequency distributions were examined during winter 1990–1991. *The 21 Dec sampling date was in 1990; all other sampling dates are in 1991. Bottom types (in addition to eelgrass): MS = muddy sand, S = sand, P = pea gravel, G = gravel, C = cobble.

Site	Sampling date(s)*	Water temp. (°C)	Depth (m) at MLW	Eelgrass density (# shoots/m ²) Mean (SD)	Bottom type	# 1/4 m ² Quadrats sampled	# Scallops sampled
N. Orient Harbor (NOH)	29 Jan, 8 Feb	3.3–4.4	1.2–1.5	628 (201)	S, G, C	11	236
East Marion (EM)	21 Dec, 2 Jan	5.6–7.1	1.3–2.0	584 (299)	S	17	224
Greenport (G)	8, 15 Mar	4.4–6.7	1.0–1.5	607 (166)	S	21	229
Off Alewife Creek (AC)	25 Mar	6.1	1.5	835 (123)	S	11	217
E. Shelter Island (ESI)	8, 11, 15 Feb	3.9–4.4	1.7–2.3	530 (158)	S, G, C	31	220
W. Shelter Island (WSI)	29 Mar, 1 Apr	7.2–7.8	1.7–2.3	353 (108)	MS	16	220
Barcelona Neck (B)	18, 26, 28 Mar	5.0–7.8	1.5–2.0	558 (92)	S, P	37	208
Sag Harbor (SH)	1, 4 Mar	3.9–6.7	0.7–1.7	686 (228)	S	26	219

in 1-m² quadrats ranged from 0–45 individuals. Mean densities at the eight sites ranged from 5.62–21.45 scallops/m² (Figure 2). An ANOVA comparing square root-transformed scallop densities was highly significant ($F = 13.89$, 7 df, $P < 0.0001$). Bonferroni multiple comparisons tests (Computing Resource Center, 1992) revealed that densities at the East Marion, North Orient Harbor, Alewife Creek, and West Shelter Island sites did not differ statistically ($P \geq 0.39$), but that the latter three sites had significantly higher densities than those at East Shelter Island, Barcelona, and Sag Harbor ($P < 0.005$). During summer 1991, mean scallop densities were dramatically lower than in the winter: 1.61 scallops/m² at Greenport

(on 24, 31 July, 2 August, and 1.73 scallops/m² at Sag Harbor on 15 August).

Shell heights of the 1773 seed scallops sampled during winter 1990–1991 ranged from 7–61 mm (Figure 3). The mean and median overall sizes were 46 and 47 mm, respectively. Mean shell heights ($n = 208$ –236) at the eight different sites ranged from 42 mm (East Shelter Island and Greenport) to 51 mm (Sag Harbor), while median heights ranged from 44 mm (East Shelter Island) to 52 mm (Sag Harbor) (Figure 3).

The scallop size frequency distributions were all negatively skewed and determined to be severely non-normal via Shapiro-Wilk tests (Computing Resource Center,

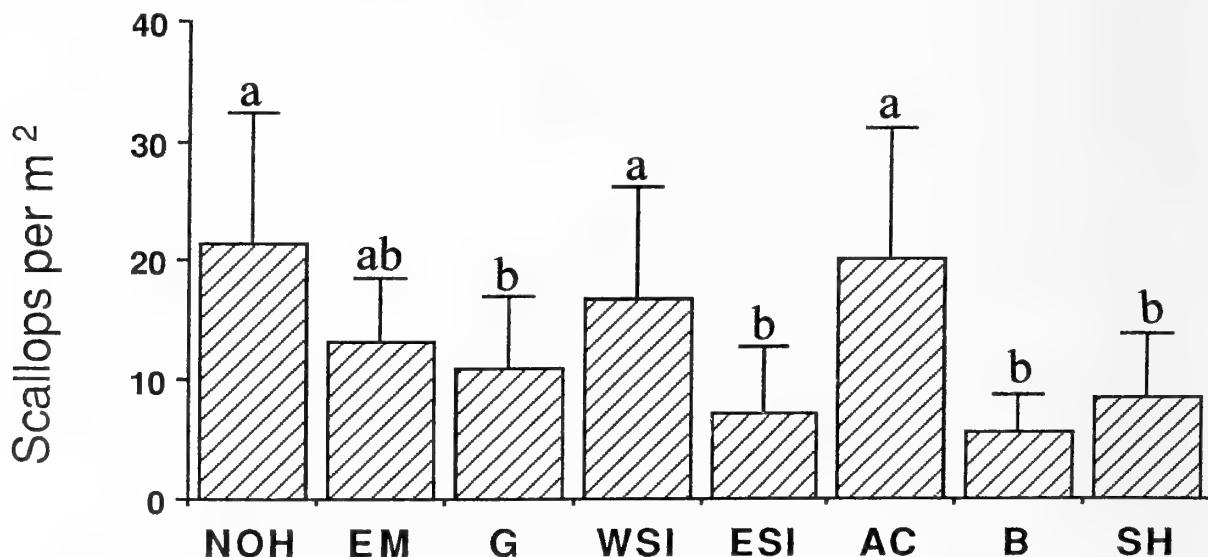


Figure 2. Mean density (+1 SD) of juvenile (0+ yr) bay scallops *Argopecten irradians irradians* sampled via diver-operated suction dredge, at each of eight sites in eastern Peconic Bays, Long Island, New York, USA during winter 1990–1991. Letters (a, b) denote differences in mean density as determined in Bonferroni multiple comparisons tests. See Table 1 for sample site abbreviations.

1992), so non-parametric analyses were necessary. A Kruskal-Wallis test demonstrated that size-frequency distributions at the eight sites (Figure 3) were not equivalent ($\chi^2 = 404.6$, 7 df, $P \leq 0.0001$). Subsequent non-parametric multiple comparisons tests (Zar, 1984) revealed that size-frequency distributions at the West Shelter Island and Sag Harbor sites were not significantly different from each other ($Q = 2.80$, 8 df, $P > 0.05$), but these size-frequency distributions were significantly different from those at the other six sites ($Q = 5.40$, 8 df, $P < 0.001$) (Figure 3).

The overall prevalence of small (≤ 20 mm) juveniles in winter 1990–1991 samples was 2.59%; the percentage of small juveniles at individual sites (Figure 3) ranged from 0% (Alewife Creek) to 8.73% (Greenport). A contingency test revealed that proportions of small juveniles at the different sites varied significantly ($G = 45.22$, 6 df, $P < 0.001$). Subdivided contingency tests (Zar, 1984) showed that proportions of small juveniles at Greenport and East Marion were not different from each other ($G = 1.0$, 1, df, $P > 0.25$), but these sites had significantly higher proportions of small juveniles than other sites ($G = 40.64$, 1 df, $P < 0.001$).

The overall prevalence of large (> 57 mm) juveniles in winter 1990–1991 samples was 2.09%; the percentage of large juveniles at individual sites (Figure 3) ranged from 0% (Alewife Creek, East Shelter Island) to 7.3% (Sag Harbor). A contingency test revealed that the prevalence of large juveniles varied significantly between sites ($G = 31.58$, 5 df, $P < 0.001$). Proportions of large juveniles in the Sag Harbor and West Shelter Island populations were not different from each other ($G = 0.56$, 1 df, $P > 0.25$), but these sites had significantly higher proportions of large juveniles than other sites ($G = 29.58$, 1 df, $P < 0.001$).

The relationship between scallop shell height and scallop density was examined via Spearman-Rank correlation tests (Computing Resource Center, 1992) because the size data were non-normal. When data from all eight sites were pooled, the H_0 (that scallop density and size are independent) was not rejected ($r_s = -0.0423$, $p = 0.0747$). However, because this value was marginally non-significant, data for each site were also examined individually. At seven of the eight sites, scallop density and size were independent ($P \geq 0.13$). At the East Shelter Island site, scallop density and size were related positively ($r_s = 0.1553$, $P = 0.0212$).

Winter-summer comparisons to examine differential mortality of small juveniles showed variable results. Of the 25 adult scallops sampled at the Sag Harbor site on 15 August 1991, only one had a growth ring < 20 mm. This proportion was not significantly different ($G = 1.08$, 1 df, $P > 0.25$) from that represented by small juveniles in the winter sample. At the Greenport site, however, where 25 of 85 sampled scallops in late July/early August had annual growth rings that were 7–20 mm from the

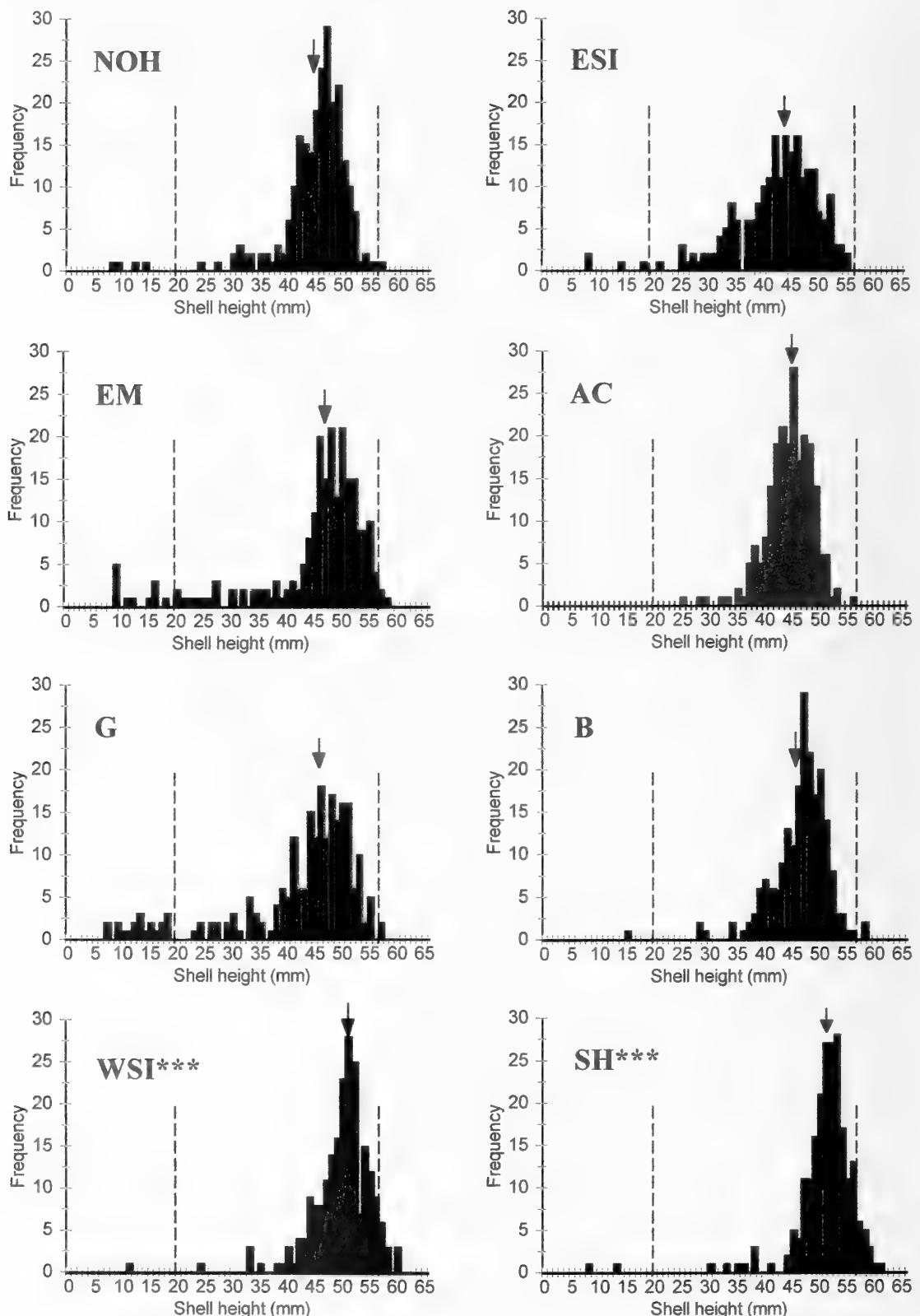
umbo, these individuals comprised a greater proportion of the summer population ($G = 18.96$, 1 df, $P < 0.001$) than that represented by small juveniles in the winter population. Seventeen adult scallops with rings between 3–6 mm also were found in the Greenport summer sample, but these were excluded from the comparison because this size range of juveniles was not retained during winter 1990–1991 suction dredge sampling.

DISCUSSION

Our comparison of scallop size variability at eight sites during 1990–1991 reflects an exceptional recruitment event. Local baymen regarded the 1990 bay scallop set to be the heaviest in the Peconic Bay system in recent memory. As compared to the overall mean density of 10.62 juvenile scallops/m² (range = 5.62–21.45/m²) which we observed in winter 1990–91, subsequent suction dredge sampling in 1994 showed that mean density of juvenile scallops ≥ 7 mm at the Alewife Creek site on 9 March was 12.8/m², while densities in late February/early March at Greenport and East Marion were 2.6/m² and 1.6/m², respectively (S. Tettelbach, unpublished data).

Estimates of scallop density obtained via suction dredge sampling are likely, in many instances, to be more accurate than those derived from dredging or visual surveys. In late September 1990, visual surveys of 0+ yr scallops at the Alewife Creek site yielded a mean density of 20.7/m² (S. Tettelbach, unpublished data), which is comparable to the 20.0/m² figure we obtained by suction dredging on 25 March 1991. However, a visual estimate of juvenile scallop density at Alewife Creek in October 1993 (≤ 4 /m²) was much lower than that reflected in suction dredge samples at the site on 9 March 1994 (12.8/m²). Many factors, including substrate characteristics (particularly the density of seagrasses and other macrophytes), scallop size, water clarity, and the experience of the observer may contribute to lower accuracy of visual censuses, relative to suction dredge sampling.

The size frequency distributions of scallops sampled via suction dredging are also likely to be different from those obtained by dredging or visual censuses. Average sizes of scallops sampled at our eight sites fell in the midst of the reported range of mean sizes of *A. i. irradians* in many previous studies, as obtained via visual sampling by divers or by scallop dredge (Belding, 1910, Marshall, 1960, Kelley & Sisson, 1981; Stewart et al., 1981; Tettelbach, 1991). However, at the Greenport site in September 1991, we determined that scallops ≤ 50 mm were significantly less likely to be retained in a bay scallop dredge with a standard bag (with 51 mm [= 2 in] rings), or when fitted with a 27 mm diagonal (3/4 × 3/4 inch square) mesh liner, compared with a suction dredge ($G = 28.66$, $P < 0.001$). It is likely therefore that average sizes of 0+ yr bay scallops reported in the literature are overestimates of true sizes in populations where small



juveniles exist. Even though we sampled seed scallops as small as 7 mm in the present study, it is likely that we still underestimated the prevalence of small seed at some sites. In 1994, when we did suction dredge sampling with a 2 mm bag (S. Tettelbach, unpublished data), one 2 mm juvenile scallop was obtained at Greenport, and 2–6 mm individuals composed 17.8% (8/45) and 8.0% (2/25) of the juveniles sampled at this site in late February and late March 1994, respectively. At East Marion, 2–6 mm individuals composed 6.7% (1/15) of the juveniles sampled in early March 1994. At the Alewife Creek site, however, no 2–6 mm juveniles were found among 204 seed sampled in early March and early April 1994. Summer 1991 sampling at Sag Harbor showed that we did not underestimate the abundance of juveniles < 7 mm in winter 1990–1991, but we clearly did at the Greenport site where there was a high prevalence of adults with annual growth rings < 7 mm from the umbo in our summer 1991 samples.

While we documented scallop densities at eight different sites in 1990–1991, it was beyond the scope of the study to determine how much these densities might have changed during the course of the winter sampling period. Suction dredge sampling in 1994, however, permitted two such estimates. In Wilcoxon rank-sum tests the mean densities of juvenile scallops ≥ 7 mm at the Alewife Creek site dropped significantly ($z = 2.90, P = 0.0037$) from $12.8/m^2$ on 9 March to $6.3/m^2$ on 6 April. Similarly, at Greenport, mean densities of juvenile scallops ≥ 7 mm dropped significantly ($z = 2.39, p = 0.0168$) from $2.6/m^2$ on 25 and 28 February to $1.1/m^2$ on 28 and 30 March. It is not known if these patterns are representative of other years.

While the reasons for the above decline in scallop densities during 1994 are not clear, the dramatic decrease in density between winter 1990–1991 and summer 1991 is likely due to mortality related to heavy infestation of scallop shells by the burrowing polychaete *Polydora* (Tettelbach & Wenczel, 1993). These worms were first noted in January 1991; their density appeared to increase through the winter. Qualitative evidence of worm-related scallop mortality in the form of high numbers of cluckers (empty shells with an intact hinge) was seen in summer 1991 but lacking in winter 1990–1991. This suggests that most of the scallop mortality occurred after the winter period. Worm densities in scallop shells in winter 1993–1994 ap-

peared qualitatively to be much lower than in winter 1990–1991.

No evidence of reduced scallop size over the observed range of densities was seen in this study. Reports of density-dependent effects in scallop populations, however, are common (see Orensanz et al., 1991). Densities at which reduced shell growth of bay scallops was evident in suspended enclosures (Duggan, 1973; Widman & Rhodes, 1991) were considerably higher than in our study. Cooper & Marshall (1963) determined that condition indexes of bay scallops in the Niantic River, Connecticut were consistently lower (although only sometimes statistically different) at a site with densities as high as $65–75/m^2$, compared to a similar habitat where densities were $\sim 11–25/m^2$. They inferred that differences in condition resulted from crowding and competition for food.

All of the size frequency distributions in the present study showed strong negative skewness, with Alewife Creek and Sag Harbor having the least and highest negative skewness, respectively (Figure 3). Several sites showed possible bi- or polymodal distributions, particularly at Barcelona, East Shelter Island, and Greenport. These types of size-frequency distributions may reflect multiple or continuous recruitment events during summer-fall 1990 and/or differential growth or mortality of different scallop sizes or groups. Multiple spawning peaks have been described in several bay scallop populations (see Barber & Blake, 1991). However, determination of the underlying reason(s) for the form of size-frequency distributions in populations is dependent on detailed knowledge of recruitment events determined through a series of samples, rather than a single sample (Ebert et al., 1993).

Small juveniles observed in our study may result from “late” spawning, a prolonged larval period and/or slow growth following larval settlement. Evidence of spawning in the Peconic Bay system during September, October, and November of several years, obtained via histological analyses (Tettelbach et al., 1999), supports the first and possibly the second mechanism. In Massachusetts, Kelley (1981), Taylor & Capuzzo (1983), and MacFarlane (1991) also provided evidence of spawning in September and October of certain years. In the latter two papers, the authors concluded that deeper water populations spawned later than those in shallower water and probably contrib-

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Figure 3. Size frequency distributions of juvenile (0+ yr) bay scallops *Argopecten irradians irradians* sampled via diver-operated suction dredge, at each of eight sites in eastern Peconic Bays, Long Island, New York, USA during winter 1990–1991. *** signify that size frequency distributions at these sites were statistically different ($P < 0.001$) from those at other sites, as determined in non-parametric multiple comparisons tests. Small (≤ 20 mm) and large (≥ 57 mm) juvenile scallop groups are demarcated by dashed vertical lines. Arrows indicate median shell heights at each site. See Table 1 for sample site abbreviations.

uted to the appearance of small seed in certain populations. Interestingly, the Greenport and East Marion sites, which had the highest proportions of small seed in this study and historically are known by baymen to be areas where small seed are often found, are located near a channel off NW Shelter Island where deep water bay scallop populations exist. Duration of the larval period of scallops is known to be prolonged at low water temperatures (Belding, 1910; Tettelbach & Rhodes, 1981; Cragg & Crisp, 1991). Given that bay scallop spawning in the fall is likely occurring at lower temperatures than in summer, the larval period may well be longer (Tettelbach et al., 1999). Further work is needed to elucidate which of the above mechanisms is most important in affecting the occurrence of small seed in winter populations.

Winter-summer comparisons to examine differential mortality of small seed at Sag Harbor and Greenport showed that small seed had an equal or lower rate of mortality than larger sizes, which is different from what might be expected on the basis of the relative susceptibility of the different size classes to crab predation (Tettelbach, 1986; Streib et al., 1995) and other factors (see Orensanz et al., 1991). Clearly, further study of the survivability of small seed is warranted.

Bay scallop populations are well known for pronounced annual fluctuations in abundance (Belding, 1910; Tettelbach & Wenczel, 1993); we suggest that small juveniles may contribute, or be essential to the persistence of bay scallop populations during certain years. This may be especially important in cases where recruitment failures occur, as has happened during brown tide algal blooms in Long Island, New York waters (Cosper et al., 1987; Tettelbach & Wenczel, 1993). A clear example of the importance of small juveniles is provided by a sample taken on 9 October 1992 at the Alewife Creek site where 100% ($n = 268$) of adult scallops sampled had growth rings which were 2–7 mm from the hinge (Tettelbach et al., 1999). These individuals were all small juveniles at the end of 1991, a year in which a 1-month brown tide bloom occurred in the Peconic Bays. MacFarlane (1991) determined that 9% of adult bay scallops in Pleasant Bay, Massachusetts in January 1980 had growth rings between 4–8 mm from the hinge; furthermore, ~50% of these individuals did not spawn in the ensuing year, but spawned the following summer. Arnold et al. (1998) have suggested that self-seeding may be necessary in order for discrete local bay scallop populations to be maintained from year to year. If a large proportion of small juvenile bay scallops survive to spawn in a second year, as suggested by MacFarlane (1991), these individuals may be particularly important because they may serve to extend the semelparous spawning of the population, and buffer the impact of a single year recruitment failure.

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NOTES, INFORMATION & NEWS

The Early Veliger Larvae of *Aegires albopunctatus* (Nudibranchia: Aegiridae), with Morphological Comparisons to Members of the Notaspidea

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Introduction

Most opisthobranchs hatch from their egg masses as planktotrophic veliger larvae with a clear unsculptured shell, an operculum, a thin foot lacking a propodium, and no eyespots (Thompson, 1976; Bonar, 1978; Todd, 1981; Hadfield & Switzer-Dunlap, 1984; Goddard, 1992, in press). As part of an ongoing survey of developmental mode in opisthobranchs from the northeastern Pacific Ocean, I examined the previously undescribed hatching larvae of the nudibranch *Aegires albopunctatus* MacFarland, 1905. These larvae are planktotrophic, but differ from other opisthobranchs with this mode of development in almost all of the characters listed above. In this note, I describe these unusual larvae and compare them to both the later stage larvae of *Aegires punctilucens* (d'Orbigny, 1837) described by Thiriot-Quiévreux (1977) and to the planktotrophic larvae of some notaspidean opisthobranchs that also lack an operculum throughout their ontogeny. *Aegires albopunctatus* ranges from British Columbia, Canada to Baja California, Mexico (McDonald, 1983; Behrens, 1991) and is the only representative of the family Aegiridae known from the northeastern Pacific Ocean.

Three specimens of *Aegires albopunctatus*, 10–12 mm long, were collected subtidally from Naples Reef, Santa Barbara County in May 2000 by Shane Anderson, and held in a 100 ml jar of filtered seawater at 14–17°C until they laid egg masses. I examined the newly laid egg masses using a compound microscope equipped with an ocular micrometer, measured the diameter of the zygotes, and then transferred the egg masses to separate vials. I changed the water in these vials daily, and examined the egg masses daily until the veligers hatched. I then examined, measured, and photographed the live hatching veligers using a compound microscope equipped with a 35 mm camera. I did not attempt to rear the larvae beyond hatching. After obtaining the above egg masses, I preserved the adults and deposited them as voucher specimens in the Department of Invertebrate Zoology at the Santa Barbara Museum of Natural History (catalogue number 345473).

Results and Discussion

Aegires albopunctatus laid white egg ribbons, 2 mm wide, in a loose spiral of one and a third turns. The mean diameter of the uncleaved eggs was 98.0 µm (SD = 1.09 µm, n = 10), considerably less than the range of 107–120 µm reported by Strathmann (1987:283) for this species from the San Juan Islands, Washington. This is probably not enough of a difference in diameter to indicate intraspecific variability in mode of development, or poecilogeny (e.g., see Krug, 1998). However, larvae obtained from the San Juan Islands should be examined for potential morphological differences from those described below. At 14–17°C, the eggs from the Santa Barbara specimens took 12.5 days to develop into hatching veliger larvae with typical coiled shells (type 1 of Thompson, 1961, and Strathmann, 1987:271), averaging 153.7 µm in length (SD = 6.40 µm, n = 5).

The hatching larvae of *Aegires albopunctatus* (Figure 1) had a strongly bilobed velum measuring up to 225 µm wide across the two lobes, and a mantle folded over the edge of the shell aperture. They were largely transparent and lacked significant yolk reserves. Their foot lacked a propodium. This set of traits unequivocally indicates a planktotrophic mode of larval development (Thompson, 1967, 1976; Bonar, 1978). However, the larvae of *A. albopunctatus* differ from the hatching planktotrophic larvae of most other species of opisthobranchs in four significant ways. (1) They lacked an operculum, had an unusually large velum, and were incapable of withdrawing completely into their shells. If disturbed, the larvae stopped swimming, folded the two lobes of the velum together like the wings of a butterfly, and withdrew only slightly into the shell. Thiriot-Quiévreux (1977) described a similar response in slightly older larvae of *A. punctilucens*, which also lack an operculum and possess a similarly large velum. (2) Although the foot of *Aegires albopunctatus* lacked a propodium, it was significantly longer, thicker, and more inflated than those of other planktotrophic opisthobranch larvae (Figure 1). It was also drawn laterally into rounded lobes that overlapped slightly the sides of the shell, and contained distally an unusual concentration of opaque white, spherical inclusions (Figure 1). These inclusions measured 10 µm in diameter and may constitute some kind of pedal gland. (3) The inner whorl of the shell had a translucent brown tinge and a wavy sculpture reminiscent of that found in patellogastropods (see Amio, 1963). (4) The veliger larvae of *A. albopunctatus* hatched with dark eyespots. Eyespots are known in the hatching planktotrophic larvae of many nu-

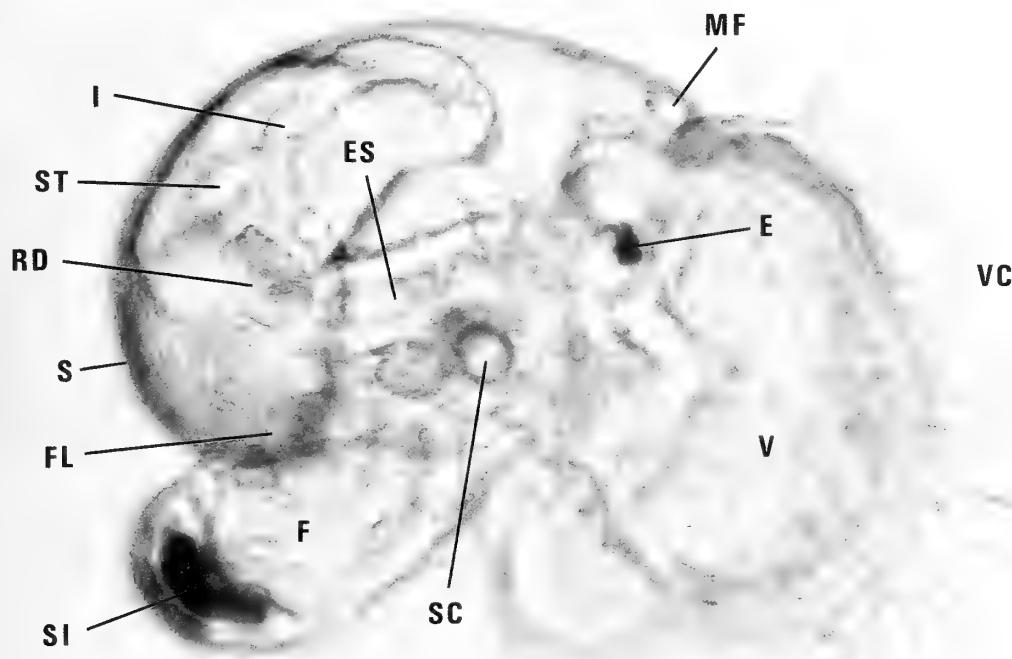


Figure 1. Live, newly hatched veliger larva of *Aegires albopunctatus*, right lateral view. The shell of this specimen was 155 µm long. The left digestive diverticulum is the large, rounded body ventral to and behind (in this view) the stomach. Bright field microscopy. Key: E, eyespot; ES, esophagus; F, foot; FL, lateral foot lobe; I, intestine; MF, mantle fold; RD, right digestive diverticulum; S, shell; SC, statocyst; SI, opaque spherical inclusions; ST, stomach; V, velum; VC, velar cilia.

dibranchs with egg-shaped, type 2 larval shells (Goddard, 1991), but are rare in the hatching planktotrophic larvae of other opisthobranchs (Thompson, 1976; Todd, 1981; Hadfield & Switzer-Dunlap, 1984; Goddard, 1992, in press).

The hatching larvae of *Aegires albopunctatus* resemble older larvae of *A. punctilucens* in the lack of an operculum and in the size of the velum relative to the size of the shell and body (Thiriot-Quiévreux, 1977). Thiriot-Quiévreux (1977) worked only with samples collected from plankton and did not describe the hatching larvae of *A. punctilucens*, so it is unknown if these larvae also hatch with eyespots. The earliest larvae Thiriot-Quiévreux (1977) examined had a flat-soled foot with an obvious propodium (see her figure 1a), but the morphology of the foot at hatching in *A. punctilucens* is not known.

Aegires punctilucens is the only benthic opisthobranch known to cast its shell during the larval stage (gymnosome pteropods, which are planktonic as adults, cast their thimble-shaped shell while still veligers [Lebour, 1931]). It then develops a juvenilike body with rhinophores, large foot, and a highly spiculate dorsum while still in

possession of a velum and swimming (Thiriot-Quiévreux, 1977). The large velum of this species is therefore likely to be an adaptation for carrying the extra weight of the developing juvenile. The similarities between the shelled larvae of *A. punctilucens* and those of hatching *A. albopunctatus* suggest that the latter may undergo a similar larval development and two-stage metamorphosis.

The only other opisthobranchs with planktotrophic development known to hatch with eyespots and to lack an operculum throughout their ontogeny are the pleurobranchacean notaspideans *Pleurobranchus* sp. from Hawaii (Ostergaard, 1950:107), *Pleurobranchaea japonica* Thiele, 1925 from Japan (Tsubokawa & Okutani, 1991), *Berthella californica* (Dall, 1900) from Oregon (Goddard, in press), and *Berthellina engeli* Gardiner, 1936, from Santa Barbara, California (personal observations). Like *Aegires punctilucens* and *A. albopunctatus*, the larvae of these species have a large velum that prevents withdrawal of the body into the shell, especially as the rest of the body grows. As in *Aegires*, the mantle of these notaspideans grows significantly during the veliger stage. However, in the pleurobranchaceans it grows to completely cover the

shell, which is retained through the benthic juvenile stage (Tsubokawa & Okutani, 1991). The pleurobranchaceans also develop rhinophores while still larvae (Tsubokawa & Okutani, 1991), but these have the longitudinal slit characteristic of the order (Willan, 1987). In addition, notaspidean larvae possess pigmented mantle organs on the right side of the body, a trait unknown in nudibranch larvae (Robertson, 1985; Goddard, 1984:147, in press).

The development and elaboration of the mantle of *Aegires* and pleurobranchacean notaspideans during their larval stage appears to have necessitated the increased locomotive power of an enlarged velum. These changes, in turn, have precluded the withdrawal of the velum and foot into the shell, and appear to have rendered the operculum useless. Why these species also hatch with eye-spots, when the vast majority of planktotrophic opisthobranchs do not, remains a mystery.

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Further Spread of the Introduced Decollate Snail, *Rumina decollata* (Gastropoda: Pulmonata: Subulinidae), in California, USA

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This note reports the occurrence of established colonies of the non-native, terrestrial decollate snail, *Rumina decollata* (Linnaeus, 1758), in San Luis Obispo County, central California, and on San Nicolas Island, Ventura County, southern California. This species is banned from San Luis Obispo County by California law. *Rumina decollata* is a detritivore, herbivore, and facultative predator on other snails. Its presence in San Luis Obispo County may pose a threat to the Morro shoulderband snail, *Helminthoglypta walkeri* (Hemphill, 1911), which is listed as endangered under the U.S. Endangered Species Act. Its presence on San Nicolas Island may harm the unique indigenous snail fauna of that island.

Rumina decollata (Figure 1) is native to the Mediterranean region of southern Europe and North Africa. It was first reported in the eastern United States in 1813 and in California in 1966 (Fisher, 1966; Fisher et al., 1980),

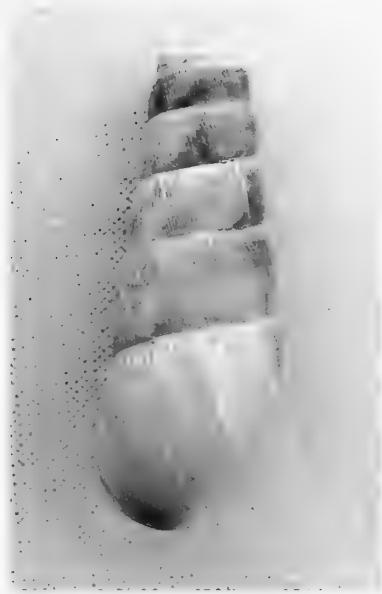


Figure 1. *Rumina decollata*, 28.4 mm specimen collected at Diablo Canyon Power Plant, San Luis Obispo County, California (LACM 152589).

though it may have occurred in California as early as 1957 or 1958 (Fisher & Orth, 1985). It has also been introduced to Bermuda, Cuba, Mexico, Central America, and Asia, and it continues to be intercepted at U.S. ports of entry (Dundee, 1970, 1974; Robinson, 1999). Its original introduction to North America presumably resulted from the transport of stowaway snails aboard ships sailing from Europe to the eastern seaboard, but its introduction to California may have been intentional, aimed at controlling the European brown garden snail, *Helix aspersa* Müller, 1774, a widespread agricultural and horticultural pest.

California state law prohibits the importation, transportation, or possession of *Rumina decollata* within all but 12 southern California counties (CDFA, 1998). Non-restricted counties include: San Bernardino, Riverside, Imperial, Orange, San Diego, Los Angeles, Ventura, Kern, Fresno, Madera, Tulare, and Santa Barbara (Figure 2). This prohibition reflects the legal status of *R. decollata* as a "detrimental animal." Detrimental animals are defined within the California Code of Regulations as those that "pose a threat to native wildlife, the agricultural interests of the state, or to public health or safety" (CDFA, 1998:document 106.4).

The life history of *Rumina decollata* is well known. Individuals may live approximately 2.5 yr, with an average lifetime fecundity of approximately 2000 eggs/individual. *Rumina decollata* is a hermaphrodite capable of self-fertilization (Selander & Kaufman, 1973; Selander et al., 1974; Selander & Hudson, 1976), although grouped individuals appear to produce more eggs than non-

grouped, i.e., self-fertilizing individuals (Fisher & Orth, 1985). Egg masses are deposited in burrows, with incubation taking 25–36 d. Following hatching, reproductive maturity is reached at approximately 12.5 mm in 75 d (Batts, 1957). During periods of adverse conditions, e.g., heat, cold, drought, *R. decollata* may become dormant, burying itself and sealing its aperture with an epiphram to prevent desiccation (Batts, 1957; Fisher & Orth, 1985). During such periods of dormancy, it may be difficult to detect in an area. When conditions are again favorable, e.g., after the start of the winter wet season in a Mediterranean climate, adults emerge to repeat the cycle.

Occurrence in San Luis Obispo County

During daylight hours on 20 January 2000, JT collected 74 *Rumina decollata* in a 20-minute period near a small ($\sim 40 \text{ m}^2$) seaside bluff at the Diablo Canyon Power Plant facility located in San Luis Obispo County, California. The animals were found on asphalt roadways and among roadside vegetation during the first substantial rainfall of the winter wet season. Although all animals observed were collected, this was demonstrably not an exhaustive search, as approximately 250 animals were collected from the same area later in January and in mid-April 2000. Most individuals collected were presumably adults based on their large sizes ($> 15 \text{ mm}$ shell height), although several smaller and possibly juvenile animals were collected. Whereas the vast majority of individuals were de-collate, several of the smaller specimens ($< 10 \text{ mm}$ shell height) retained their apical whorls. Since 1992, JT had consistently observed *R. decollata* at this location during and following the first substantial rainfall of the season. Whether it occurred here prior to JT's initial site visit and observation in 1992 is not known. The site is highly disturbed because of past construction activities, and is characterized by ruderal, roadside vegetation (e.g., *Hirschfeldia incana*, *Foeniculum vulgare*) and remnant stands of native coastal bluff scrub (e.g., *Hazardia squarrosa*, *Atriplex* spp.) growing on fill soils. Voucher specimens from Diablo Canyon are deposited at the Santa Barbara Museum of Natural History (SBMNH 345670) and the Los Angeles County Museum of Natural History (LACM 152589).

Occurrence on San Nicolas Island

San Nicolas Island is under the control of the United States Navy. *Rumina decollata* was discovered there in February 1983 by Pearce (1993:41, Loc. 8). It was found in a small grove of planted pine and cypress trees ("Fernandez Grove") on the north side of the main naval compound. Fernandez Grove is one of the few horticulturally tended, artificially watered areas on the island; according to a sign, the trees were planted in October 1967. Around sprinklers, tall grass and *Sonchus* sp. were present. Live adult and juvenile snails were sparsely present in the soil



Figure 2. Known distribution of *Rumina decollata* in California. Dots indicate occurrences noted by Fisher & Orth (1985). Arrows indicate locations of feral populations at Diablo Canyon Power Plant, San Luis Obispo County (top), and San Nicolas Island, Ventura County (bottom). Twelve (12) shaded counties are those where *R. decollata* is legally permitted for release.

under the layer of pine needles carpeting the grove. At that time, considerable search elsewhere among the buildings of the compound and in the adjacent native scrub vegetation did not reveal any other occurrence of the species. It was absent from numerous other sites on the island that were inspected for land snails then and in later years (Pearce, 1993; BR, unpublished data). Observation of *R. decollata* in the pine grove was repeated by Pearce, BR, and others in 1984, 1985, 1986, and 1992.

In June 1998, BR, Alicia Cordero, and David Lindberg observed *R. decollata* to have spread into native *Coreopsis gigantea* scrub on the 100-m terrace north of the naval compound and just east of the rim of the first canyon east of Celery Canyon. This is approximately 0.4 km from the Fernandez Grove. One living specimen and about 10 empty shells were observed in a 2-hour search; some shells bore marks of small mammal predation, probably by deer mice, *Peromyscus maniculatus exterus*.

Discussion

Pest eradication without using chemicals is intuitively appealing, and biocontrol has consequently emerged as an important tool to control non-native and undesirable plants and animals. One has only to search the Internet to get an idea of the scale and breadth of this industry that has formed under the rubric of Integrated Pest Management. Several sites on the World Wide Web advertise *Rumina decollata*—available for about \$25.00 US per 100 animals—as a “natural,” and therefore preferable, alternative to poisoning *Helix aspersa*. Densities of approximately 1000 *R. decollata* per 0.4 ha are suggested to eradicate *H. aspersa* in 3–4 years.

Claims of eradication may be exaggerated: *Rumina decollata* preys on other snails up to approximately 15 mm shell diameter (T. W. Fisher, oral communication to BR, March 1977). Individual snails that reach a larger size are effectively immune from predation. Therefore, complete eradication of *H. aspersa* is rarely achieved; instead, its numbers are reduced to those individuals that escape predation as young but remain present and continue to reproduce. Furthermore, *R. decollata* does not prey solely on *H. aspersa*; it will eat most snail species presented to it (Fisher & Orth, 1985; T. A. Pearce, personal communication, 2000; BR, unpublished observations). *Helix aspersa* and the native snail species *Helminthoglypta umbilicata* (Pilsbry, 1898)—both abundant throughout the coastal terraces of the Diablo Canyon Power Plant site—are absent, except for a few empty shells, from the area occupied by the colony of *R. decollata*. Predation by *R. decollata* on eggs or young of these snail species is a possible explanation, but additional field observation is needed.

The rate of active dispersal by *R. decollata* depends at least partly on the frequency, type, and duration of irrigation. Fisher et al. (1980) reported a maximum dispersal

rate of 20 m in 3 months in an irrigated orchard. Our observations on San Nicolas Island indicate a minimum rate in unirrigated native scrub of 0.4 km in 12 years. The Diablo Canyon colony site is also unirrigated, and it appears that the *R. decollata* population may be somewhat localized, though no distribution data were collected. Despite efforts on numerous occasions to locate *R. decollata* in vegetation approximately 1 km inland from the identified colony, JT has been unable to do so.

The expansion of *Rumina decollata* within California is likely related more to passive (anthropogenic), rather than active, dispersal mechanisms. Although warning statements prohibiting the delivery of *R. decollata* to addresses in many California counties are widely disseminated, snails are easily ordered from Internet-based businesses and advertisements in organic gardening magazines. Malacologists have long recognized that there is essentially unregulated anthropogenic dispersal of *R. decollata*.

The present distribution of *Rumina decollata* in California is unknown. Fisher & Orth (1985) mapped *R. decollata* within 14 California counties (Figure 2), and noted that “Special rulings by [the] California Fish and Game Commission permitted [a] study [of *R. decollata*] to be pursued in the counties of Butte, Del Norte, Fresno, and Sacramento, as well as 8 counties south of the Tehachapi Mountains” (Fisher & Orth, 1985: viii). Feral colonies of *R. decollata* were known prior to 1983 within all but two (Madera and Santa Barbara) of the 12 presently authorized southern California counties, and within two presently unauthorized central California counties: Santa Clara and Merced. In 1996, *R. decollata* was found feral on open ground near the San Diego River (Roth & Hertz, 1997) in a location that received no irrigation.

The mechanism of introduction of *Rumina decollata* to the power plant location is unclear. Access to the utility-owned property is largely restricted to employees, and this rural facility site is located approximately 12 km from the nearest urbanized area. It is doubtful that anyone would have intentionally introduced *R. decollata* to the site, and less likely that someone would have intentionally introduced it only on the grassy bluff to which the colony appears to be limited. Thus, unintentional transport of *R. decollata*, e.g., attached to equipment, drop-boxes, lumber, or perhaps as eggs in fill soil is suspected as a mechanism of introduction to this location.

Of great concern is the fact that the Diablo Canyon colony of *Rumina decollata* is located approximately 9 km south of the remaining population of the endangered Morro shoulderband snail, *Helminthoglypta walkeri*, near the town of Los Osos. Land development already has reduced the range of *H. walkeri*, and introduction of *R. decollata* to this region could result in additional harm to this protected species. Despite the apparently limited potential for colony range expansion, efforts should be made to determine the distribution of *R. decollata* in

San Luis Obispo County, and eradication efforts undertaken as necessary.

The potential is great for harm by *R. decollata* to the unique, endemic land snail fauna of San Nicolas Island. Among the strictly endemic native snails, *Micrarionta opuntia* Roth 1975, never attains a shell diameter of more than about 10.3 mm; the mean adult shell diameter of *Micrarionta feralis* (Hemphill, 1901) is around 15 mm (Pearce, 1990; Roth, 1996). For these species, the "refuge" of a size greater than 15 mm diameter (which allows *Helix aspersa* to persist at low numbers in the presence of *R. decollata*) is unavailable. In addition, the total known range of *M. feralis* covers only a few hundred square meters.

The San Nicolas Island species *Xerarionta tryoni* (Newcomb, 1864) attains an adult shell diameter of 19–28 mm. Size-frequency distribution of a population observed in 1981 suggests that maximum shell size and sexual maturity are attained late in the second or early in the third year of life. A shell diameter of 15 mm is probably not attained until the second year of life (BR, unpublished observations). Time to maturity in *Helix aspersa* varies, but in a coastal southern California setting with artificially applied water, snails matured in 6–8 months (Potts, 1975). Under laboratory conditions, a shell diameter of 15 mm was attained in about 25–45 days (Potts, 1975: fig. 2). Juvenile *Xerarionta tryoni* spend more time in the vulnerable < 15-mm size class than do juvenile *Helix aspersa*, and therefore the potential impact of predation upon populations of *X. tryoni* is greater than that recorded for *H. aspersa*.

The apparent localization and slow spread of *Rumina decollata* on San Nicolas Island suggest that its eradication on that island may be possible.

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The Occurrence of the Shell-Less Neritacean Gastropod *Titiscania limacina* in the Galapagos Islands

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Only two species of shell-less neritacean gastropods of the family Titiscaniidae have been described: *Titiscania limacina* Bergh, 1875, and *T. shinkishihataii* Taki, 1955. The former was discovered and drawn by Carl Semper during his voyage to the Philippines, and it was first named by Bergh (1875; pl. 41, fig. 10) based on Semper's figure. Later, Bergh (1890) published a complete description based on additional specimens from Mauritius. This species has been also recorded in the Eastern Pacific Ocean from the Gulf of California to Panama (Marcus & Marcus, 1967; Houston, 1990; personal observation); in the Eniwetok Atoll (Marcus & Marcus, 1967); in north-

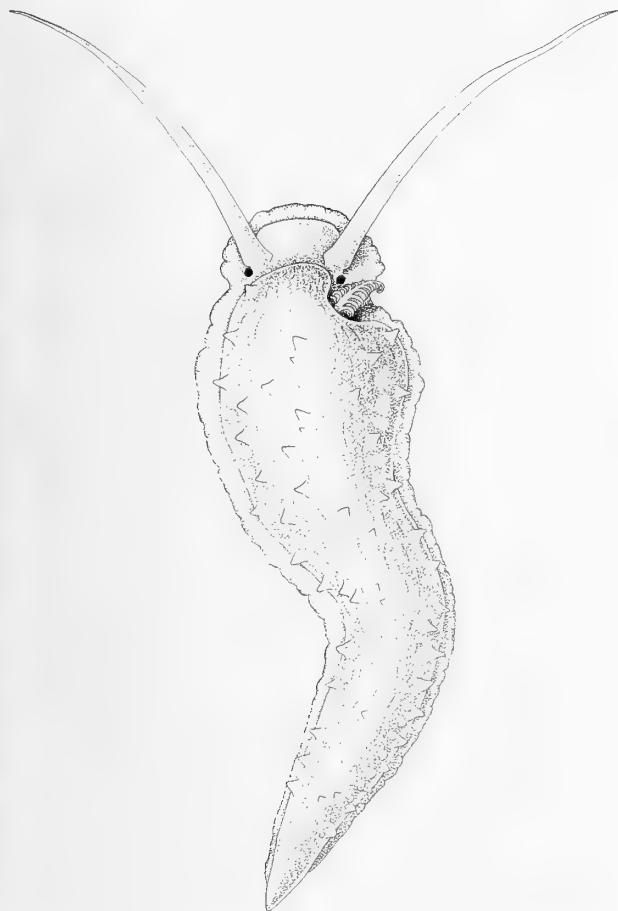


Figure 1. Specimen of *Titiscania limacina* from Puerto Ayora, Santa Cruz, Galapagos Islands (17 mm in length).

east Australia (Burn, 1975); and in the Molucas (Strack, 1998). Taki (1955) described the second species of this genus in Japan, *Titiscania shinkishihataii*, which was rediscovered and redescribed by Saito & Tsuchiya (1990). The differences between both species might not be considered specific characters because some minor differences have also been found in specimens from distant geographic areas, perhaps as a result of their different stage of conservation or as a consequence of the methods used to study the slugs. Therefore, both taxa might be synonyms. Nevertheless, according to Scott & Kenny (1998), the Titiscanidae remains a poorly known group with few specimens available for study.

Titiscania limacina, despite being a shallow-water gastropod recorded from the west American continental coast and from some eastern Pacific islands, is not known from any of the eastern Pacific oceanic islands, as pointed out by Emerson (1991) in his study on the tropical trans-Pacific prosobranch gastropods. The malacofauna of the Galapagos Islands is, without doubt, the best studied of all eastern Pacific islands (see the reviews of Finet, 1991,

1994). However, *Titiscania limacina* has never been recorded there until now.

During a Spanish scientific trip to the Galapagos Islands in 1991, organized by the Museo de Ciencias Naturales de Tenerife, Canary Islands, three specimens of this species were found. These specimens were collected off Puerto Ayora, Santa Cruz Island, in front of the Charles Darwin Research Station (6 March 1991). The three specimens were found beneath intertidal rocks, covered by white compound ascidians of the family Didemnidae. They measured alive 11, 14, and 17 mm when crawling. At resting position they were notably shorter. The external appearance of our specimens (Figure 1) does not differ from other descriptions of the species. These elongate sluglike animals were white in color with a row of 10–12 opaque white papillae along each side of the notum. A white defensive secretion was expelled from these papillae when the animals were disturbed. Some isolated papillae were also present on the notum. The cephalic tentacles were long, thin, and sharply tapering. They became abruptly narrower just at their bases. Small eyes were located at the outer bases. The ctenidium projected partially from the opening of the mantle cavity near the head and somewhat toward the right side. The foot was translucent and wide, extending well beyond the notum, with its anterior end expanded into a pedal veil. The three specimens are deposited at the Museo de Ciencias Naturales de Tenerife, Canary Islands.

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International Commission on Zoological Nomenclature

The following Applications concerning mollusks were published on 30 March 2001 in Volume 58, Part 1 of the *Bulletin of Zoological Nomenclature*. Comment or advice on any of these applications is invited for publication in

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Case 3158. *Helix lucorum* Linnaeus, 1758 and *Helix punctata* Müller, 1774 (currently *Otala punctata*; Mollusca, Gastropoda): proposed conservation of usage of the specific names by replacement of the syntypes of *H. lucorum* with a neotype.

Case 3175. *Ampullaria canaliculata* Lamarck, 1833 (currently *Pomacea canaliculata*; Mollusca, Gastropoda): proposed conservation of the specific name.

The following Opinion concerning mollusks was published on 30 March 2001 in Volume 58, Part 1 of the *Bulletin of Zoological Nomenclature*. Copies of Opinions can be obtained free of charge from the Executive Secretary, I.C.Z.N., c/o The Natural History Museum, Cromwell Road, London SW7 5BD, U.K. (e-mail: iczn@nhm.ac.uk).

Opinion 1965. *Euchilus* Sandberger, 1870 and *Stalioa* Brusina, 1870 (Mollusca, Gastropoda): *Bithinia deschiensiana* Deshayes, 1862, and *Paludina desmarestii* Prévost, 1821 designated as the respective type species, with the conservation of *Bania* Brusina, 1896.



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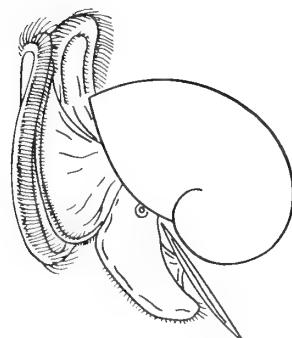
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